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Environmental influences on larval fish condition in Antarctic costal waters

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ENVIRONMENTAL INFLUENCES ON LARVAL FISH CONDITION IN ANTARCTIC COASTAL WATERS

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By
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ABSTRACT

ENVIRONMENTAL INFLUENCES ON LARVAL FISH CONDITION IN ANTARCTIC COASTAL WATERS

by Edward A. Laman

Three species of larval Antarctic fishes collected from Gerlache Strait, Bransfield Strait, and Marguerite Bay (*Lepidonotothen larseni*, *Trematomus newnesi*, and *T. lepidorhinus*) were characterized on the basis of morphometric nutritional condition indices which were compared with respect to hydrographic features within these regions. The three nutritional condition indices analyzed were yolk reserve size, gut fullness, and relative condition factor. The variable nature of the relationship between larval length and weight yielded a relative condition factor with little predictive power. Variations in nutritional condition for these species resulted from growth trajectories following the advancing season and demonstrated environmental forcing in only a single case. Regional differences in nutritional condition reflect species-specific horizontal and vertical distribution patterns. Overall, the highest condition factors occurred among larvae collected from the center of each species' distribution. Changes in larval condition attributable to the advancing season were more influential than between-year differences among these Antarctic larval fishes.

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INTRODUCTION

Parrish and Mallicoate (1995) use the term "environmental forcing" to describe the effects of such factors as food availability, water temperature, depth, salinity, circulation patterns, and population density on metabolic processes of fishes. During the vulnerable pelagic stages of development, these influences on larval nutritional condition combine with sources of mortality to determine subsequent year class strength (Marshall 1953; Lasker 1981; Huntley and Niiler 1995). Therefore, relative nutritional condition within an ichthyoplankton assemblage may reflect localized, seasonal, or perhaps interannual effects of environmental forcing and is the focus of the present study.

There are limited types of biological data that can be used to assess the influence of environmental forcing on fish survival and recruitment. One type of data attainable for many fish populations is condition factor, usually defined as the observed weight of a fish divided by the expected, or average weight, of a fish of the same length based on length/weight regression analyses (Le Cren 1951; Parrish and Mallicoate 1995). Complementary to condition factor, and of particular importance to young Antarctic fishes, is the duration of the yolk-sac phase (Kellermann 1990; Laman and Loeb 1994). Measures of nutritional condition and yolk utilization reflect a synergy among food availability, environmental forcing, and behavior of the larvae and represent the cumulative impact of metabolic processes occurring over a scale of perhaps several days (Theilacker 1986). Because Antarctic notothenioid larvae hatch with substantial yolk reserves, the prolonged resorption period preserves yolk reserve size as a potential indicator of prior feeding history. Thus, a third factor which aids in understanding the nutritional condition of Antarctic fish larvae is a measure of feeding rate. Larval fish prey density and predator/prey encounter rate are largely determined by environmental factors such as depth of the thermocline, retention zones, and food availability; these help to structure the incidence and rate of feeding within an ichthyoplankton assemblage.

Few studies have investigated the feeding ecology of early stage Antarctic fishes. Kellermann (1986) focused on the feeding ecology of post-larval and juvenile *Pleuragramma antarcticum*. Kellermann (1990) investigated larval *Lepidonotothen larseni* and found that their feeding habits change seasonally. North and Ward (1989) described feeding by the larvae of four fish species at South Georgia (*Trematomus hansoni*, *Harpagifer georgianus*, *Parachaenichthys georgianus*, and *Pseudochaenichthys georgianus*). North and Ward (1990) also investigated the larval feeding ecology of *Champsocephalus gunnari* and four other species which are important to the finfish industry at South Georgia. Prey types varied in all of these studies but were primarily copepod eggs and nauplii, euphausiid eggs, and other larval fishes. None of these studies discussed feeding rates with respect to condition, yolk utilization, or environmental forcing.

Physiological adaptations controlling respiratory and metabolic processes such as growth and yolk-sac utilization also influence the survival of individual larvae. Kellermann (1990) hypothesized that observed differences in the incidence and size of yolk reserves of larval *Lepidonotothen larseni* may have resulted from spatial and temporal variations in the planktonic environment and/or early feeding success. Kellermann (1990) also speculated that long yolk resorption times among Antarctic larval fishes relative to temperate or boreal fish larvae (Kock and Kellermann 1991) may enable them to survive extended periods of poor food availability in the highly variable Antarctic marine environment. He further suggested that the relatively slower growth rates of Antarctic larvae compared to some temperate species may act in concert with the extended yolk resorption times to spread the nutritional demands of the larvae over a greater period of time. It is during this critical window in their early life history that survivorship to subsequent stages of development is determined (Lasker 1981).

Antarctic fishes have other adaptations for increased survivorship in the harsh and variable conditions of the Antarctic marine ecosystem. Within the marginal sea-ice zone surrounding the continent, ice cover inhibits primary production by limiting the amount of solar radiation available for photosynthesis and its retreat in spring initiates the brief and intense spring/summer bloom period (El-Sayed 1985; Comiso et al. 1990; Knox 1994). The extent of the seasonal sea-ice cover is temporally and geographically variable and, as a result, the onset of the spring bloom can be delayed during some years (Foster 1984; North and White 1987). The extreme seasonality of the phytoplankton bloom and subsequent secondary production increase, combined with low levels of primary production during winter months are among the strongest selective pressures acting on Antarctic ichthyofauna. Reproductive adaptations to these conditions are demonstrated by large, developmentally advanced larvae which can feed exogenously upon hatching and are endowed with substantial yolk reserves to compensate for the temporally and spatially variable onset of the spring production cycle (Everson 1984; North and White 1987; Kellermann 1990). Many of these early life history adaptations are shared with benthic invertebrates and have been generalized as "Thorson's Rule" (Ruzicka 1996): large eggs; large developmentally advanced larvae; relatively slow growth; and reproductive efforts synchronized with the spring bloom (Thorson 1950; Arnaud 1977; White 1977; Clarke 1979, 1983; North and White 1987; Kellermann 1989a). Most Antarctic fishes also have pelagic larval stages of varying duration (days to several years). Their larvae hatch year-round, but peaks in diversity and abundance generally coincide with spring and summer periods of elevated secondary production (Kellermann 1989a). There is also evidence that temporal succession of hatching events in the Southern Ocean may act to reduce inter- and intraspecific competition for shared resources during the brief spring production cycle (Kellermann 1989a; Kock and Kellermann 1991).

The unique adaptations of Antarctic fishes are the result of the long evolutionary history of the Antarctic marine ecosystem. Approximately 140 million years ago (Ma) Antarctica was part of the Gondwana land mass and was positioned in low southern temperate latitudes (Elliot 1985; Lawver et al. 1985). As Gondwanaland began to fragment, the Antarctic and Australian plates separated from the other major continental land masses and ca. 80 Ma Antarctica was established in its present polar position (Lawver et al. 1985; Figure 1). Around 53 Ma the Tasman Sea had formed and Australia had begun to separate from Antarctica. However, the South Tasman Rise still blocked any major current system from developing between the two continents. Around 39 Ma, major climate changes precipitated dramatic lowering of south polar temperatures, Antarctic glaciation became established, and extensive sea-ice developed. Approximately 25-28 Ma the South Tasman Rise separated sufficiently from Victoria Land for the Antarctic Circumpolar Current to become established. The Drake Passage opened between South America and Antarctica around 25-14 Ma (Kennett 1977). With the establishment of the Circumpolar Current, the Antarctic Convergence formed at ca. 22 Ma creating a faunal barrier isolating the Southern Ocean from the Pacific, Atlantic, and Indian Oceans (Kennett 1977, 1978, 1980; Kerr 1984, 1987; Clarke and Crame 1989; Dayton 1990).

Fossil records from Seymour Island near the tip of the Antarctic Peninsula indicate that the contemporary ichthyofauna of the Southern Ocean originated from a relatively diverse coastal assemblage that was well established by ca. 40 Ma. Disappearance of these forms and their replacement by present day species over the past 30 million years appears to be the result of rapid cooling events and the formation of sea ice (Eastman 1991, 1993). Fish species which failed to adapt to the new temperature regime were replaced by ones that developed antifreeze glycopeptides (Devries 1968, 1982; Devries and Wohlschlag 1969) and attendant biochemical and physiological adaptations to low temperatures. Other processes such as habitat and faunal destruction resulting from glacial advance may have

aided in the extinction of earlier species; lack of recolonization was likely the result of geographic isolation and the faunal barrier presented by the formation of the Antarctic Convergence (Eastman and Grande 1989 ; Clarke 1979, 1983). The result of these processes has been the evolution of a fish assemblage dominated by a few, endemic teleost families. Reflecting their demersal origins, these fishes are represented by primarily bottom-dwelling adult forms, many with pelagic larval stages which presumably enhance dispersal.

Families of the perciform suborder Notothenioidei dominate the coastal adult fish assemblages. These are primarily endemic to Antarctic waters with 86% of the known species distributed south of the Antarctic Convergence. The five most common notothenioid families in nearshore assemblages are Nototheniidae (notothens), Channichthyidae (icefishes), Bathydraconidae (dragonfishes), Artedidraconidae (plunderfishes), and Harpagiferidae (spiny plunderfishes); the larvae of these also dominate the ichthyoplankton (Loeb et al. 1993). Because of their high abundance, notothenioids have an important role in the trophic structure of coastal ecosystems as intermediate links between primary production and top predators (Croxall and North 1988). Nototheniids and channichthyids have also been the subjects of targeted fisheries which have dramatically reduced stock sizes, affected species composition, and changed size-frequency distributions over the past 30 years (Kock 1985; Kock et al. 1985). Because of their key role in the trophic structure of coastal Antarctic ecosystems, as well as their dominance and importance as a fishery species, notothenioids are the focus of most ichthyoplankton research in the Southern Ocean (North 1991; Loeb et al. 1993).

The larval fishes featured in the present research (*Lepidonotothen larseni*, *Trematomus newnesi*, and *T. lepidorhinus*) are members of the family Nototheniidae, perciform suborder Notothenioidei, which characteristically spawn demersal eggs with pelagic larvae (Kellermann 1989a; Gon and Heemstra 1990). They are endemic to the

Southern Ocean (Loeb et al. 1993) and adults of these species are found primarily in coastal and shelf waters (Kellermann 1989b; Tiedtke and Kock 1989) dominating the ichthyofaunal assemblages of the Antarctic continental shelf regions (Gon and Heemstra 1990). Adult *L. larseni* and *T. newnesi* are common in the Seasonal Sea-ice zone while *T. lepidorhinus* has been characterized as a High Antarctic (i.e., high latitude) species in the marginal sea-ice zone (Kock and Kellermann 1991) which possibly accounts for its rarity in previous surveys of the Gerlache Strait region (Loeb 1993). Larvae of *L. larseni* and *T. newnesi* are seasonally collected in high abundance in plankton samples from Gerlache Strait (Laman and Loeb 1993; Loeb 1993) and the Antarctic Peninsula region in general (Kellermann and Kock 1988; Kellermann 1989 a, b). These three species often numerically dominate the nearshore ichthyoplankton assemblage and are abundant as adults in continental shelf communities. Their abundance and dominance indicate that they play an important role in the trophic structure of these coastal Antarctic fish communities.

This study was part of the multidisciplinary, National Science Foundation Office of Polar Programs Research on Antarctic Coastal Ecosystem Rates (RACER) project designed to examine factors responsible for enhanced phytoplankton biomass and productivity in coastal relative to offshore waters and to assess the significance of this enhanced primary productivity to higher trophic levels (Huntley et al. 1990). Ichthyoplankton samples for the present research were derived from two RACER cruises during two separate years. The RACER II sampling program, conducted in October-November 1989, targeted the onset of the early spring phytoplankton bloom in the elevated productivity regime within Gerlache Strait (Huntley et al. 1990). The December 1991-January 1992 RACER III sampling program concentrated on factors associated with the demise of the phytoplankton bloom in late spring and its resulting effects on local zooplankton assemblages in Gerlache Strait. The overall objective of the ichthyoplankton component of the RACER program was to

evaluate the role of productive neritic regions in supporting ichthyoplankton assemblages relative to offshore Bransfield Strait waters (Loeb 1993; Loeb et al. in press).

The objectives of this study were to: (1) develop series of condition indices for three numerically dominant ichthyoplankton species *Lepidonotothen larseni*, *Trematomus newnesi*, and *T. lepidorhinus*; (2) compare these series with relevant physical and biological factors; (3) develop hypotheses concerning how these physical and biological factors may affect condition factors, yolk utilization rates, and feeding rates and, by implication, the energetics of ichthyoplankton assemblages in Gerlache and Bransfield Strait waters.

METHODS

Sampling

The RACER program studies were designed to determine if elevated levels of zooplankton abundance and primary production in Gerlache Strait during the 1986-1987 RACER pilot study were due to accumulation resulting from physical processes or originated there through high rates of local reproduction, growth, and survivorship. These questions were addressed by targeting the zooplankton assemblages with an extensive program of vertically stratified sampling within Gerlache Strait and the southwestern Bransfield Strait (Figures 2 & 3). Physical (salinity, temperature, depth) and biological (chlorophyll-*a* concentration) oceanographic data were collected concurrently at each station using a Seabird SBE-9 CTD (Amos et al. 1990). The present study focuses on the larval fish component of the zooplankton collections from the RACER program.

Zooplankton was collected in the Antarctic Peninsula region (Figure 1) during two RACER cruises aboard R/V "Polar Duke". The early spring RACER II cruise (30 October - 23 November, 1989) targeted the peak of the spring primary production bloom (Huntley et al. 1990). The late spring/early summer RACER III cruise (12 December 1991 - 3 January 1992) targeted the demise of the spring phytoplankton bloom (Holm-Hansen and

Vernet 1990). Three nototheniid species, *Lepidonotothen larseni, Trematomus newnesi,* and *T. lepidorhinus*, numerically dominated RACER II ichthyoplankton (Loeb 1992) and are the subjects of this study.

Sampling during both cruises was conducted in Gerlache Strait and adjacent Bransfield Strait waters; additional sampling took place at the Marguerite Bay ice-edge during RACER III (Figure 1). Net sampling operations were conducted with a Multiple Opening Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al. 1976, 1985) using 333 μm black Nitex™ mesh. During RACER II, vertically stratified tows were made over a 4000 km^2 grid of stations (36 "F" series stations) at approximately one week intervals (Figure 2). Vertically and horizontally stratified tows were made at a time series station "A" in eastern Gerlache Strait after each "F" series grid was sampled. The same sampling methodology, with only vertically stratified tows at station "A", was applied over a slightly different station grid in Gerlache Strait and within Marguerite Bay during RACER III (Figure 3). Lower depth limits of the nine vertically stratified samples from each tow were 5, 15, 50, 90, 130, 170, 210, 250, and 290 m; in shallower water, samples were collected beginning with the standard depth interval closest to the bottom. The horizontally stratified samples from RACER II were collected from a 15-50 m depth stratum. A more detailed description of RACER sampling protocol is given in Huntley et al. (1990).

Potentially different environmental regimes affecting larval fish nutritional condition were identified based on the hydrography of Gerlache Strait (Laman and Loeb 1994; Figure 4) during spring 1989. The hydrography was characterized by a swift axial current (ranging from 15 to 60 cm · sec^{-1}) flowing from southwest to northeast with a coastal mesoscale eddy flanking it to the south in the vicinity of station "A" (Lopez et al. 1993). Three regions were distinguished based on the hypothesis that different feeding conditions

might exist within this hydrographic setting. These regions were defined as: (1) the bays (Hughes, Charlotte, and Wilhelmina Bays); (2) station "A" (located in the mesoscale eddy between the bays and axial current); and (3) axial current (remaining stations in the Strait and/or main axial flow exiting into Bransfield Strait; Laman and Loeb 1995).

Yolk Reserves

Yolk reserves are a significant source of nutrition to young fishes. Their size, the result of yolk utilization, may represent prior feeding history and thus act as an estimate of condition. Yolk-sac perimeter and area were measured simultaneously using an image analysis system (Image 1.37-National Institute of Health) linked to a Macintosh™ computer via television microscopy and a mouse-controlled cursor to outline the yolk-sac (Figure 5). A specific surface area index (SSA) modified from that of McFadzen et al. (in prep.) was calculated as,

$$SSA = \frac{Y_1/Y_2}{NL},$$

where Y_1 is yolk area, Y_2 is yolk perimeter, and NL is notochord length. Within each sampling period, values of SSA were compared for each species among depth strata, length classes, and regions using multivariate analysis of variance (MANOVA; Tabachnick and Fidell 1996). Incidence of yolk-sac larvae was calculated for each species as the proportion of larvae with yolk reserves out of the total number collected. Proportional changes in the incidence of yolk-sac larvae were compared between seasons (sampling years) and among regions.

Feeding

Gut fullness (F) and feeding incidence (F_i) were measured to assess feeding rates. Guts were removed under a dissecting microscope. Gut fullness was estimated for three regions {fore (F_f), mid (F_m), and hindgut (F_h)} using a subjective scale of 0 to 5 (0=empty,

5=full; Cailliet and Ebeling 1990; Kellermann 1990). The overall index of gut fullness, F, was calculated by combining the three separate indices,

$$F = F_f + F_m + F_h \quad .$$

Feeding incidence for each species was calculated as the percentage of guts containing food out of the total number of guts examined; these values were contrasted between seasons (sampling years) and among geographic regions. The complete early spring (RACER II) data set was used to assess diel periodicity of recent feeding bouts, indicated by the presence of food in the foregut. Three-way ANOVA's were used to compare the arcsine-transformed F_f values for each species among three daily light cycles: day; night; crepuscular. Values of F within seasons (sampling years) were compared among depth strata, length classes, and regions using MANOVA.

Relative Nutritional Condition Factor

In order to develop a meaningful relative nutritional condition factor, larval fish growth was assumed to conform to the Le Cren's (1951) equation,

$$W = a \cdot L^b,$$

where W is weight (in this case dry weight), L is some morphometric index (commonly standard or notochord length) measured on the larva, a is a proportionality constant and b is a scaling exponent, both empirically derived. This equation is a modification of the first condition factor equation proposed by Fulton (1904) based on the assumption that fish growth is isometric (i.e., $W=L^3$). The relative condition factor (k) is then the ratio of weight to length following Le Cren's (1951) equation,

$$k = \frac{W}{aL^b}.$$

The term $a \cdot L^b$ is the predicted weight of a fish of length (L) based on the regression between length and weight for the sampled population. When the measured weight of the larva approaches its weight predicted from the regression equation, k approaches unity.

By combining the methods of Koslow et al. (1985) and Theilacker (1986), morphometric indices were generated from three food deprivation sensitive and three food deprivation insensitive measurements collected from individual larvae using television microscopy and the image analysis system. Direct measurements of the deprivation sensitive indices were: notochord length (*NL*); body height at the pectorals (*BP*); and body height at the anus (*BA*). The deprivation insensitive indices were: eye diameter (*ED*); head length (*HL*); and interorbital distance (*IO*; Figure 6). These combined measurements formed five ratios (*BP/NL, BA/NL, ED/NL, HL/NL, IO/NL*) totaling 11 morphometric indices to regress against dry weight (*DW*). Backward-stepwise multiple regression analysis (Zar 1984) determined which of the 11 morphometric indices described the greatest within-sample variation when regressed with *DW*. This was performed on larvae collected during RACER II and yielded the variable *L* in Le Cren's equation. The other components of Le Cren's equation, the proportionality constant (*a*) and scaling exponent (*b*), were estimated from combined RACER II and RACER III data sets by iterative non-linear regression analysis (SYSTAT 1992). An implicit assumption of this approach is that relationships predicting relative condition factor are conserved over time and space (i.e., geographical distributions). For each species, a series of relative condition factors was used to assess temporal (seasonal/interannual) and regional trends; this method was similar to that of Parrish and Mallicoate (1995). Relative condition factors within years were compared among depth strata, length classes, and regions using MANOVA.

To obtain dry weights, individual larval fish were placed on pre-weighed foil pieces (ca. 1 cm by 2 cm) and dried to a constant weight. They were placed in a drying oven at 60°C for 48 hours, removed, and then transferred to a desiccator for 24 hours (personal communication Martin White, British Antarctic Survey, Cambridge, UK; Mary Yoklavich, NOAA/NMFS Pacific Fisheries Environmental Group, Pacific Grove, CA). The combined

weight of the foil and desiccated larva was measured using a Perkins/Elmer™ micro-balance; subtracting the tare of the foil yielded dry weight of the larva.

Environmental Data

Depth-specific environmental data from each station consisted of temperature (°C), salinity (parts per thousand, $^{o}/_{oo}$), and chlorophyll-*a* concentration (chl-*a*, mg / L) which could be linked to individual larvae. These variables were used in MANOVA's to test whether larval fish condition was affected by hydrographic conditions. Values of these environmental variables were analyzed from the mid-point depth of each vertical sampling stratum and were thus linked to the depth-specific collection of individual larvae. Although naupliar copepods and euphausiid eggs are common prey items of many Antarctic larval fishes (Barrera Oro and Tomo 1986; Kellermann 1987, 1990; North and Ward 1989, 1990) and could have given a direct measure of food available to the larvae, their abundance and composition in the MOCNESS samples were not readily available. Large population increases of small herbivorous zooplankton in the Antarctic typically result from the seasonal increase of primary production (North and White 1987; Kock and Kellermann 1991). Therefore, primary production estimates based on chl-*a* were chosen as a proxy for the predicted increase in secondary production following the seasonal bloom (Huntley et al. 1990).

Statistical Analyses and Data Collection

All statistical analyses were performed using SYSTAT (1992) and a Macintosh™ computer. Univariate data were compared using ANOVA's (Zar 1984). Data which did not conform to the assumption of homogeneity of variance were subject to transformation; if transformation failed to conform the data, non-parametric ranking techniques such as the Kruskal-Wallis ANOVA were employed.

MANOVA

Two-way MANOVA's were used to compare groups of dependent variables among three multi-level independent variables in two tests (depth of capture × larval length; depth of capture × region). Due to widely varying presence/absence of the larval fishes and incomplete data records for environmental parameters, only a limited number of observations were available for comparisons made after randomization and resorting necessary to create similar sized data blocks. As a consequence, depth strata were used twice employing the Bonferroni correction for multiple passes through the data (Zar 1984; Tabachnick and Fidell 1996). The two groups of dependent variables were condition measures (SSA, F, and k) and environmental parameters (temperature, salinity, and chlorophyll-*a*). The three independent variables were depth strata (three levels), larval fish length classes (three levels), and regions (three levels in RACER II and four levels in RACER III). Three depth strata were selected based on the average midpoint depth of occurrence for each species. These were: 0-15 m, 15-50 m, and 50-290 m for *Lepidonotothen larseni* (mean depth 75.7 m) and *Trematomus lepidorhinus* (mean depth 16.6 m); and 0-5 m, 5-15 m, and 15-290 m for *T. newnesi* (mean depth 11.4 m). Length classes for each species were selected from examination of size-frequency distributions from RACER II samples; groupings were applied to later season RACER III collections to maintain comparability. The smallest and largest size classes combined represented 15-30% of the length-frequency distribution; the middle size class was the remaining 70-85% of larvae. Length classes were: 6-9 mm, 9-13 mm, and > 13 mm for *L. larseni*; 7-13 mm, 13-16 mm, and > 16 mm for *T. newnesi*; and 5-7 mm, 7-10 mm, and > 10 mm for *T. lepidorhinus*. Three regions common to both cruises were the bays (Charlotte, Hughes, and Wilhelmina Bays), station "A" (location of the coastal eddy during RACER II), and the axial current in Gerlache Strait. Marguerite Bay was sampled only during RACER III.

Prior to conducting MANOVA's, data were screened for multicollinearity and balanced sample sizes. Pearson correlation matrices were generated within dependent variable groups using SYSTAT so that multicollinear variables ($|r| > 0.7$) could be eliminated from further analyses. Where numbers of observations within a comparison grouping (e.g., medium-sized larvae collected from the 0-5 m depth stratum in all regions) were unequal by a ratio $\geq 4:1$, randomization and resampling were employed to allocate the numbers of observations for a balanced design. Homogeneity of variance (HOV) assumptions were tested with Bartlett's test (SYSTAT 1992). Tabachnick and Fidell (1996) stated that the MANOVA remains robust if the ratio of the greatest to smallest variance within a dependent variable group does not exceed 10:1. If data did not conform to either the HOV assumptions or Tabachnick's and Fidell's (1996) ratio criteria, transformations were employed (e.g., $\log(x+1)$, $(1/x)$); data were ranked when transformations failed. When appropriate, significant results from the MANOVA were subjected to *a priori* comparisons to specify significant effects in a stepdown analysis (Tabachnick and Fidell 1996).

RESULTS

Sampling

During early spring (RACER II), 103 tows in Gerlache Strait and adjacent Bransfield Strait waters (Figure 2) yielded 1,578 larvae representing 19 fish taxa. Three nototheniid species (*Lepidonotothen larseni*, *Trematomus newnesi*, and *T. lepidorhinus*) numerically dominated and constituted 84% of the total averaged abundance (Table 1; Loeb 1993). Nutritional condition studies of these collections utilized data from 589 *L. larseni*, 573 *T. newnesi*, and 220 *T. lepidorhinus* larvae.

Collections from late spring (RACER III) included 115 tows from the Gerlache Strait area (Figure 3a) and 13 tows on a line normal to the ice-edge in Marguerite Bay (Figure 3b). A total of 778 larvae were collected in the Gerlache Strait area and 2,390 in

Marguerite Bay. Larvae from the two regions again represented 19 taxa. In Gerlache Strait, *T. lepidorhinus* and *L. larseni* were the first and second numerically dominant species and *T. newnesi* was the seventh most abundant taxon. In Marguerite Bay, *T. lepidorhinus* was the second most abundant taxon after *Pleuragrammaantarcticum*, followed by *T. newnesi* and *L. larseni* (Table 2; Loeb 1995). Nutritional condition studies were made on 274 *L. larseni*, 53 *T. newnesi*, and 661 *T. lepidorhinus* larvae from these collections.

Lepidonotothen larseni

There were apparent between-season (interannual) and within-season (regional) differences in yolk utilization by *L. larseni* (Figure 7). Overall, the mean yolk reserve sizes ($\overline{SSA}$) were larger in early vs. late spring ($p<0.001$) indicating depletion with the advancing season. Larvae collected in the axial current during early spring had the largest $\overline{SSA}$ values followed by larvae from the coastal eddy in early spring and then by all larvae collected in late spring. In late spring, $\overline{SSA}$ values for larvae from the axial current and coastal eddy were indistinguishable. In addition, the proportion of *L. larseni* with exhausted yolk reserves in both regions increased from early to late spring; this increase was from 37% to 71% in the axial current and from 23% to 66% at station "A". Direct comparisons of $\overline{SSA}$ between seasons at the bay stations and in Marguerite Bay were not possible due to the absence of *L. larseni* larvae in the bays during late spring and the lack of replication in Marguerite Bay. The proportion of larvae with exhausted yolk reserves was 14% in the bays during early spring and 25% in Marguerite Bay in late spring.

Mean gut fullness ($\overline{F}$) of *L. larseni* larvae increased significantly from early to late spring ($p=0.003$; Figure 8). The $\overline{F}$ values of larvae from the axial current and at station "A" were indistinguishable in both seasons. Feeding incidence (F_I) also increased with

advancing season. At station "A", F_t increased from 66% during early spring to 92% in late spring; F_t in the axial current increased from 62% to 93% over the same period. Larvae collected from the bays during early spring had a relatively lower F_t (50%) than those from the other two regions during that time. Similarly, larvae from Marguerite Bay had a relatively lower F_t (75%) than larvae from the other three regions during late spring.

Comparison of recent feeding, evidenced by food in the foregut (F_f), of *L. larseni* larvae between diel light cycles (day, night, and crepuscular) using a nonparametric Kruskal-Wallis ANOVA indicated no significant differences (p=0.430). Larvae collected during day, night, and crepuscular periods exhibited average F_f frequencies of 13%, 15%, and 22%, respectively. The frequent occurrence of empty foreguts and lack of knowledge regarding gastric evacuation rates make it difficult to resolve diel periodicity in feeding behavior for these larvae despite the likelihood that they, like most larval fishes (Lasker 1981), are visual predators.

Backward-stepwise multiple regression analysis of 11 morphometric indices derived from *L. larseni* larvae (Appendix I) indicate that notochord length (NL) is the best predictor of dry weight (DW) for this species. Values for the proportionality constant (b) and scaling exponent (a), as estimated by iterative non-linear regression, compare favorably with Le Cren's (1951) predictions. The proportionality constant (b=1.952) is close to Le Cren's predicted range of 2.0- 4.0 and a is estimated as 0.005. The final form of the equation is

$$k = \frac{DW}{0.005 \cdot NL^{1.952}},$$

which has a significant correlation coefficient of 0.89 (p<0.050).

Regional and seasonal (inter-annual) differences in the range and magnitude of k were apparent as were underlying patterns of distribution (Figure 9). Only seven *L. larseni* larvae occurred in the bay stations during early spring and none were collected there during

late spring. Relative condition factors of larvae collected from the coastal eddy (station "A") and axial current stations were similar to each other within each sampling period. Larvae at station "A" during late spring had significantly higher $\bar{k}$ values than those collected there in early spring (1.26 > 0.85; $p<0.001$). However, mean notochord lengths ($\overline{NL}$) at station "A" were not significantly larger in the late vs. early spring. Mean relative condition factor and $\overline{NL}$ of larvae in the axial current exhibited a pattern opposite to that observed at station "A"; $\bar{k}$ values were not significantly higher in the late vs. early spring but $\overline{NL}$ was significantly larger during the later season (11.8 mm vs. 10.2 mm; $p<0.001$). Only five *L. larseni* larvae were collected in Marguerite Bay samples, but the range of k for these larvae was within that of other regions sampled that season. Trends in k-values appear related to regional variation or to large scale temporal changes (i.e., seasonal/inter-annual), but with no clear relationship to time within either season.

ANOVA and MANOVA Results (*L. larseni*)

There were significant effects of capture depth, length classes, and regions on larval *L. larseni* condition during early spring (Figure 10; Appendix II). Mean yolk reserve sizes decreased, $\overline{F}$ increased, and $\bar{k}$ remained constant with increased larval length indicating that yolk utilization resulted from growth and was independent of feeding success or relative condition. Yolk reserve sizes and $\bar{k}$ values were also much higher in the axial current than at station "A", but $\overline{F}$ was not significantly different between the two regions indicating that there may be a higher energetic cost to larvae within the coastal eddy. One effect which did not vary relative to other measures of condition (i.e., no multivariate significance) was $\bar{k}$ which was significantly higher for *L. larseni* larvae collected from 50-290 m ($p=0.001$) relative to the two shallower strata. The effect was independent of region or larval length.

Significant effects of depth and region on environmental factors associated with *L. larseni* larvae in early spring resulted primarily from changes in chl-*a* values (Figure 11; Appendix II). The marked decrease in chl-*a* between the 0-15 and 15-50 m strata relative to the steady decline in temperature and increase in salinity with depth yielded a significant multivariate effect. Similarly, multivariate significance between regions resulted from lower chl-*a* in the axial current combined with relatively little difference between temperature or salinity there and at station "A". These results were duplicated in the univariate effects tests. Larvae collected from the two deeper strata were significantly associated with increased salinities ($p<0.001$) in the axial current and the coastal eddy ($p<0.001$). A similar significant trend was observed for low chl-*a* values associated with *L. larseni* larvae in the two deeper strata ($p<0.001$), but with no regional differences.

Unlike results from early spring, there were few significant relationships among condition measures during late spring (Appendix III). As during early spring, relative condition of *L. larseni* larvae showed a significant dependence on depth ($p=0.009$), but this relationship was reversed with the lowest relative condition factor exhibited by larvae from 50-290 m ($p=0.003$). The vertical distribution pattern of larval *L. larseni* abundance observed earlier in the season with maximum abundance at station "A" (Loeb 1993) was less distinct in late spring which may explain this apparent trend reversal.

Similar to early spring, relationships among environmental factors associated with larval *L. larseni* in late spring were depth-dependent, varied among regions, and their multivariate significance was due primarily to marked changes in chl-*a* (Figure 12; Appendix III). Temperature and chl-*a* values decreased ($p=0.002$ and $p<0.001$, respectively) while salinity increased with depth of capture ($p<0.001$). The significant regional difference in chl-*a* concentration ($p=0.012$) was not supported by more conservative multiple comparison tests indicating that these differences were marginal.

However, the relative difference in chl-*a* among regions was sufficient to yield a significant multivariate effect.

Trematomus newnesi

Trematomus newnesi larvae showed obvious yolk utilization between early and late spring (Figure 13). Similar to *L. larseni*, $\overline{SSA}$ decreased significantly between early and late spring sampling periods in both the coastal eddy (p=0.024) and axial current (p=0.008). In all three regions compared, the proportions of larvae with exhausted yolk reserves also increased in the later season: from 11% to 33% in the bays; 21% to 40% at station "A"; and 16% to 50% in the axial current. *Trematomus newnesi* collected in Marguerite Bay exhibited the lowest proportion of post yolk-sac phase larvae of any region sampled during late spring (23%).

Like *L. larseni*, *T. newnesi* larvae collected during late spring were better fed than those collected earlier (Figure 14). Mean gut fullness in late spring was significantly higher than during early spring at both station "A" (p=0.002) and in the axial current (p=0.001); $\overline{F}$ of larvae in Marguerite Bay was also relatively high in late spring. Feeding incidence (F_i) of *T. newnesi* larvae increased seasonally in the bays (91% to 100%) and axial current (80% to 100%), but remained relatively stable at station "A" (92% and 91%). Larvae in Marguerite Bay had F_i = 100%.

Similar to results for *L. larseni* larvae, ANOVA indicated that there was no significant diel difference in the occurrence of recent feeding bouts of *T. newnesi* larvae (p=0.770). *Trematomus newnesi* larvae exhibited average F_f values of 37% during day, 44% during night, and 44% during crepuscular periods; these values are about twice that of *L. larseni* indicating that these larvae fed more often. Lower gastric evacuation rates for these larvae may invalidate the assumption that food presence in the foregut indicated a

recent feeding bout. In addition, high coefficients of variation for F_f values among the three light cycles (82-97%), resulting from a large number of zeros in the dataset, further obscure any statistical significance.

Backward-stepwise multiple regression analysis of *T. newnesi* morphometric indices indicate that, like *L. larseni*, NL is the best predictor of DW (Appendix I). Values for b and a also compare favorably with Le Cren's predictions. The proportionality constant (b=3.25) is within the predicted range and a is estimated to be 0.0003. The final form of the equation is

$$k = \frac{DW}{0.0003 \cdot NL^{3.25}},$$

which has a significant correlation coefficient of 0.96 ($p<0.050$).

Regional and seasonal (inter-annual) differences in the range and magnitude of larval *T. newnesi* condition factors were apparent as were seasonal (inter-annual) differences in regional occurrence (Figure 15). Numerous *T. newnesi* larvae were collected in Charlotte, Hughes, and Wilhelmina Bays during early spring (n=145), but only three individuals were collected from these bays during late spring. No statistical comparison can be made between bay samples from the two seasons (years) due to unequal sample sizes and uneven replication. Mean lengths of the few larvae collected in the bays during late spring were larger than those in early spring (15.8 mm vs. 14.0 mm). Larvae collected at station "A" during late spring had significantly higher condition than those collected earlier in the season (1.08 vs. 0.53; $p<0.001$) despite no significant increase in $\overline{NL}$ between the two periods. In contrast, both $\overline{NL}$ and $\bar{k}$ of larvae from Gerlache Strait stations increased significantly from early to late spring; 13.7 to 15.4 mm ($p<0.001$) and 0.52 to 1.50 ($p<0.001$), respectively. Although *T. newnesi* larvae collected in Marguerite

Bay during late spring had greater $\overline{NL}$ than those in Gerlache Strait, the $\bar{k}$ was not notably higher.

ANOVA's and MANOVA's comparing *T. newnesi* condition

All three measures of larval *T. newnesi* condition were significantly dependent upon capture depth and region for larvae collected during early spring (Appendix II). The significant univariate interaction between depths and regions for $\overline{SSA}$ ($p<0.001$) and the significantly higher $\overline{F}$ values at 5-15 m and at station "A" ($p=0.003$ and $p=0.004$, respectively) reflect the significant multivariate interaction between depths and regions (Figure 16). Gut fullness was highest in the 5-15 m strata at both station "A" and in the axial current. However, $\overline{SSA}$ from this stratum was lower at station "A" relative to the axial current. Since $\bar{k}$ values at 5-15 m were the same for larvae at station "A" and in the axial current, larvae at station "A" possibly required more energy to maintain the same level of condition.

Environmental factors associated with *T. newnesi* larvae during early spring showed significant depth dependence and some evidence of environmental forcing on condition (Appendix II). Temperature varied with larval length ($p=0.001$). Salinity exhibited univariate interactions between depths and length classes ($p=0.009$) as well as between depths and regions ($p<0.001$). Chlorophyll-*a* concentration also varied as a function of depth strata and length classes as indicated by the significant interaction ($p=0.001$). Both temperature and chl-*a* varied significantly between regions; highest mean temperature ($p<0.001$) and chl-*a* ($p<0.001$) were associated with larvae collected at station "A". Salinity varied as a function of depths and regions indicated by their significant interaction ($p<0.001$). Additionally, there were significant multivariate interactions between depth strata, length classes, and regions (Figure 17). The interaction between depth strata and larval length resulted from relatively low chl-*a* in the 0-5 m stratum

associated with smaller larvae and the warmer water associated with larger larvae at 5-15 m depths. A multivariate interaction between depth and region resulted from an influx of warm, low salinity water containing high chl-*a* concentration at 5-15 m depths at station "A" (coastal eddy) and to a lesser extent in the axial current.

Physical oceanographic variables associated with *T. newnesi* larvae during late spring primarily reflect the inclusion of Marguerite Bay samples (Appendix III). Larvae collected in Marguerite Bay were associated with low salinity ($p<0.001$) high chl-*a* ($p<0.001$) melt-water characteristic of the transitional ice-edge zone (Knox 1994). Significant multivariate effects on environmental factors resulted from changing relationships among depth strata and regions (Figure 18). When depth strata were considered, chl-*a* values remained the same and salinity increased with depth. Salinity was much lower and chl-*a* much higher at the Marguerite Bay ice-edge reflecting the presence of highly stratified meltwater and indicating a large phytoplankton crop (Karl et al. 1992).

Trematomus lepidorhinus

Decreased mean yolk reserve sizes from early to late spring indicated that larval *T. lepidorhinus* absorbed yolk during the course of the season ($\overline{SSA}$; Figure 19) as did *L. larseni* and *T. newnesi* larvae. Yolk reserves decreased significantly in bays ($p=0.013$) and were completely depleted at station "A" by late spring. The proportions of larvae with exhausted yolk reserves increased seasonally in both the bays (17% to 33%) and at station "A" (25%-44%), but decreased in the axial current from 66% to 8%. In contrast, 100% of *T. lepidorhinus* larvae collected in Marguerite Bay were still in the yolk-sac phase.

Feeding incidence (F_i) increased seasonally in the bays (43% to 50%), station "A" (24% to 55%), and axial current (0% to 53%). Feeding incidence for *T. lepidorhinus* larvae in Marguerite Bay in late spring was substantially lower than that recorded in other

regions during that time (19%). The observed lower feeding rates in Marguerite Bay combined with the overall high incidence and size of yolk-sac reserves and the presence of recently hatched individuals (NL≈6.0 mm; Kellermann 1989b) indicate that this region may be a nursery ground for *T. lepidorhinus* (Loeb et al. in press).

Foregut feeding incidence (F_f) indicated that these larvae did not feed in the dark. The average frequency of larvae with food present in the foregut was 4.2% in daylight, 0% at night, and 3% during crepuscular periods. However, these apparent differences were not statistically significant. Overall, feeding incidence for these larvae is substantially lower than that of larval *L. larseni* or *T. newnesi*. As with these other two species, the lack of information on gastric evacuation rates for *T. lepidorhinus* larvae precludes any definitive conclusion regarding diel feeding periodicity or visual predation from these data.

In contrast to the other two species, a predictive relationship between a morphometric index and *DW* was not established for *T. lepidorhinus* larvae. Graphical analyses of these data demonstrated that length-based morphometric indices alone were insufficient to describe the variation in *DW* (Figure 20).

ANOVA's and MANOVA's comparing *T. lepidorhinus* condition

Gut fullness of *T. lepidorhinus* larvae was significantly dependent on capture depth in early spring (see Appendix II). Larvae collected from depths >15 m had significantly larger amounts of food in their guts than those in shallower depth. The significant multivariate effect of depth for $\overline{F}$ and $\overline{SSA}$ may indicate poor feeding conditions and/or greater energetic demands for *T. lepidorhinus* larvae in the near surface waters (Figure 21).

Chlorophyll-*a* concentrations associated with *T. lepidorhinus* larvae during early spring were also significantly affected by depth (Appendix II). Temperature and salinity were excluded from these analyses due to multicollinearity. In addition, only larvae from station "A" were analyzed due to insufficient numbers from other regions. Chlorophyll-*a*

concentrations were significantly greater in the 0-15 m stratum than in deeper strata ($p<0.001$).

Condition of *T. lepidorhinus* larvae during late spring was depth-dependent, varied significantly with larval length and region, and exhibited several significant multivariate effects (Figure 22; Appendix III). Mean yolk reserve sizes were greatest for larvae from the 50-290 m stratum ($p<0.001$) and were smallest for the largest larvae analyzed (7-10 mm; $p<0.001$). Mean gut fullness was lowest for larvae collected from the 50-290 m stratum ($p<0.001$). The highest $\overline{F}$ values coincided with the lowest $\overline{SSA}$ values reflecting a development-dependent relationship with decreasing $\overline{SSA}$ and increasing $\overline{F}$ with increasing larval length. Larval lengths were not significantly different between station "A" and the axial current but lengths were significantly greater in Marguerite Bay ($p=0.010$) than in these other regions. *Trematomus lepidorhinus* larvae at station "A" had the highest $\overline{F}$ and lowest $\overline{SSA}$ values compared with other regions suggesting an increased energetic cost to larvae at station "A".

Environmental factors associated with *T. lepidorhinus* larvae during late spring varied significantly with capture depth, larval length, and region and exhibited several significant multivariate effects (Figure 23; Appendix III). Both temperature and chl-*a* decreased ($p<0.001$ for both) and salinity increased ($p<0.001$) with depth of capture. Temperatures associated with small 5-7 mm larvae were significantly lower than those associated with larger larvae ($p=0.002$). Larvae collected from Marguerite Bay were associated with significantly lower temperatures ($p=0.004$) and higher chl-*a* concentrations ($p<0.001$). Associated temperatures were not distinctly different in Gerlache Strait, but larvae at station "A" were collected from waters with significantly higher chl-*a* values than those in the axial current ($p=0.001$). Associated salinities interacted significantly between depth and region ($p=0.002$) reflecting low values in the surface water at the Marguerite Bay

ice-edge. *Trematomus lepidorhinus* larvae near the surface (0-15 m) were associated with higher temperatures, lower salinities, and higher chl-*a* concentration than those from depths ≥15 m. Smaller larvae were found at greater depths and were, therefore, associated with cooler temperatures. Finally, larvae from Marguerite Bay were associated with cold, low salinity melt-water which contained the highest chl-*a* values recorded in the RACER II and III samples.

DISCUSSION

It is hypothesized in this work that variations in the nutritional state of Antarctic larval fishes result from environmental forcing either directly, such as temperature effects on physiology (Blaxter 1992) or early feeding success (Kellermann 1989), or indirectly, such as regional variation attributable to horizontal advection (Cowen et al. 1993; Huntley and Niiler 1995). High measures of nutritional condition reflect optimal feeding regimes and indicate that the larvae have a higher potential to survive than larvae with low condition factors. Optimal feeding regimes are likely determined in large part by hydrography and the physical accumulation of both larval fishes and their prey in a particular area (i.e., indirect environmental forcing). Unique features of the early life history of Antarctic fishes combined with the relative constancy of their environment (Knox 1994) appear to make them particularly suited for examination of nutritional condition and environmental forcing due to the strongly seasonal nature of reproductive efforts and food availability in the coastal regions. Specifically, their large yolk reserves and seasonally discreet hatching periods (possibly excepting *T. lepidorhinus*; Loeb et al. in press) lend themselves to detecting changes in larval condition. However, additional factors not studied here (e.g., larval behavior and metabolic rates) likely play a large role in determining condition of these larvae.

Kellermann et al. (in press), hypothesized that the extended yolk resorption period in Antarctic larval fishes results from early initiation of feeding rather than slowed metabolic rates associated with the low ambient temperatures. This prolonged yolk-sac stage allowed the use of yolk reserve size as an indicator of prior feeding success and as a morphometric index of nutritional condition. In late spring, larvae of *L. larseni* and *T. newnesi*, which have seasonally discreet hatching periods (North and White 1987; Kock and Kellermann 1991; North 1991; Laman and Loeb 1993; Loeb et al. 1993), exhibited significant yolk depletion relative to larvae collected earlier in the season. *Trematomus lepidorhinus*, which appear to have prolonged and multiple hatching periods (Loeb 1995; Loeb et al. in press), also showed evidence of yolk depletion with advancing season.

The significant increase in the proportion of yolk-sac *T. lepidorhinus* larvae in the axial current during late spring may have resulted from an influx of newly hatched individuals swept into Gerlache Strait in the strong southwest to northeast flow (Niiler et al. 1990; Lopez et al. 1993). Depletion of yolk reserves in *L. larseni* and *T. newnesi* larvae from Gerlache Strait by late spring was accompanied by increased F, F_t, and k values and increased larval lengths; the F_t value and length of *T. lepidorhinus* larvae also increased in conjunction with the seasonal depletion of yolk reserves. Differences in condition of *L. larseni* and *T. newnesi* larvae between early and late spring appear to result from growth and development. Even though *T. lepidorhinus* appear to undergo an extended hatch period, significant differences between early and late spring larvae were primarily due to increases in larval length.

In Gerlache Strait, where distributions of the numerically dominant larval fish taxa roughly coincide with regional hydrography (Loeb 1993), it appears that species-specific energetic requirements are best met for larvae found in the center of their horizontal and vertical distributions (Laman and Loeb 1995). Loeb (1992) found that the dominant larval fish taxa had species-specific depth distributions in early spring. Among the three species

considered here, *L. larseni* larvae had the deepest distribution center and were most abundant in the axial current (Loeb 1993); these had the best nutritional condition (highest k and largest SSA) compared with those in other regions and depths that season. *Trematomus newnesi* has the most robust larvae of the three species. These larvae occurred at the shallowest depths, and exhibited condition that was independent of their vertical and horizontal distribution patterns. The vertical distribution center of *T. lepidorhinus* during early spring, 15-50 m, was intermediate to those of the other two species. Condition of these larvae was highest for larvae in the center of their vertical distribution irrespective of region; these had the largest yolk reserves and highest condition factor and their gut fullness decreased with depth.

Several researchers have shown that metabolic and developmental rates of larval fishes can be affected by simple hydrographic features such as temperature (Blaxter 1992; Clarke et al. 1992; Holmes and Youson 1994) and/or salinity (Kilgour et al. 1994). Adequate nutrition can also affect larval ontogenesis (Clarke et al. 1992). The clockwise current gyre located at station "A" during early spring was selected as one of the three distinct hydrographic regions in Gerlache Strait under the assumption that it might represent a different larval feeding regime and potentially one of enhanced prey availability due to entrainment and retention (Laman and Loeb 1993). None of the three species examined demonstrated higher gut fullness or feeding incidence values in the station "A" gyre during early spring. In fact, for the statistical analyses indicate that *T. newnesi* larvae in the gyre were not as well fed as those in other regions. These larvae were also exposed to relatively warm (~0.5 °C), low salinity water in the center of their depth distribution (i.e., 5-15 m). As a result, these larvae in both regions, given the same levels of gut fullness, exhibited increased yolk utilization at station "A" and thus maintained the same levels of nutritional condition among regions. The apparent increased energetic cost to larvae at station "A"

may result from elevated temperatures, variations in salinity affecting buoyancy and inducing physiologic stress, or a combined affect of these.

Antarctic larval fishes are highly stenothermic as a result of their long history of exposure to low amplitude temperature variation (Knox 1994). Therefore, temperature can affect nutritional condition of larval fishes in the Southern Ocean more than in other regions. Increased yolk utilization, as observed for *T. newnesi* larvae associated with elevated temperatures, could result from increased metabolism/respiration and/or accelerated enzymatic activity in the warmer water (Clarke et al. 1992). Johnston (1993) demonstrated that resting and maximum metabolic rates of adult *Notothenia coriiceps* were positively correlated with environmental temperature. Accelerated yolk resorption could lead to increased mortality of larvae presented with insufficient food resources. Variations in salinity may increase physiologic stress by affecting buoyancy of the larva, thus increasing the energetic cost to remain at their optimal depth.

During late spring, there were no significant relationships with larval condition and the environmental factors measured indicating a change relative to earlier in the season. There were fewer larvae in Gerlache Strait (Loeb 1995) and species-specific depth distribution patterns were less distinct. These changes may be the result of seasonally decreased larval production, mortality of early life stages, advective loss, settlement, and/or migration of later larval stages from the study area. Measures of *L. larseni* and *T. newnesi* condition were independent of vertical and horizontal distribution in late spring and were unaffected by the three environmental forcing factors examined. The lack of significant multivariate differences in late spring may partly be caused by the apparent disintegration of species-specific depth distributions in Gerlache Strait. Also, the smaller sample sizes would reduce the power of the statistical analyses to detect differences. Differences in the nutritional condition of these two species relative to early spring samples reflect larval growth and development which resulted in larger, more robust larvae that were presumably

less susceptible to environmental conditions. In contrast to *L. larseni* and *T. newnesi*, condition of *T. lepidorhinus* larvae remained dependent upon vertical and horizontal distribution in late spring reflecting the presence of mixed-size cohorts as well as the inclusion of the abundant larvae from Marguerite Bay samples.

There is some evidence for inter- and intraspecific resource partitioning as a result of the utilization by different sized larvae of different size-fractions of their prey population (Balbontin et al. 1986; Kellermann 1986, 1989a). Besides the segregation of trophic niches by larval size variation, and the species-specific depth distributions of the larvae (Loeb 1992), there is a temporal sequence of hatching periods throughout summer (Kock and Kellermann 1991) which is thought to be related to the occurrence of calanoid copepod reproduction peaks (Kellermann 1986, 1989a). Despite the appearance of resource partitioning which may reduce competition for shared prey resources among Antarctic larval fishes, there is little evidence to suggest that food limitation is an overriding issue in coastal waters during the seasonal bloom (J. Barry, MBARI, personal communication). Thus, the apparent partitioning through succesional hatching events or distinct vertical distributions may be indicative of previous competition and, subsequently, relative condition factors based on somatic growth of Antarctic larval fishes may be independent of environmental forcing in Gerlache Strait during spring.

Röpke (1993) showed that vertical distributions of some mesopelagic larvae in the Arabian Sea are structured by their prey. Research on the feeding habits of Antarctic ichthyoplankton indicate that their prey are primarily naupliar copepods and krill eggs, although some species are piscivorous (Kellermann 1987, 1990; North and Ward 1989, 1990). Spawning cycles of the invertebrate prey taxa are synchronized with the seasonal ice break-up and subsequent spring phytoplankton bloom (Huntley et al. 1994). Their reproductive products are vertically distributed in the water column by developmental stage

(Lopez et al. 1993; Nordhausen 1992, 1994) which equates to size and may structure the vertical distributions of the ichthyoplankton which are dependent on them.

In a recent study, Cowen et al. (1993) found that simple hydrographic parameters (e.g., salinity, temperature) explained only ca. 15% of the observed variability in larval fish species distribution and assemblage membership within the mid-Atlantic Bight. These researchers concluded that a more detailed accounting of other factors was required to accurately assess distributions and to adequately explain observed variations. These factors include: spawning location; patterns of larval transport; presence, persistence, and location of physical features such as fronts or currents; predation; and larval behavior. In a dynamic region such as Gerlache Strait, it is apparent that the simple hydrographic and biotic features chosen for this study (i.e., temperature, salinity, and chl-*a*) would need to be supplemented with additional factors such as those listed above to resolve evidence of environmental forcing within the ichthyoplankton community. This would require finer scale sampling of oceanographic data as well as sampling specifically directed at the ichthyoplankton assemblage in the region. The latter might be aided by identifying, following, and sampling the same water mass over time using an acoustic doppler current profiler (ADCP) or by following Lagrangian drifters.

The scale of the RACER program sampling design was not well suited for assessing the detailed relationships between larval fish condition and environmental forcing. In addition, the assumption about the enhanced productivity of coastal regions in the Antarctic (Huntley et al. 1990) was not properly tested by sampling known oligotrophic waters such as those in the Drake Passage. Replication was uneven and incomplete, limiting the power of statistical comparisons (Zar 1984; Tabachnick and Fidell 1996). Future studies examining environmental influences on larval fish condition in the Antarctic must be designed on a finer spatial and temporal scale and should provide for more consistent replication of sampling stations. Sampling would have to be conducted over a

greater time span than a single season and must include comparison with oligotrophic waters such as Drake Passage.

Aspects of larval behavior (e.g., vertical and horizontal migration) must be considered when drawing conclusions based on nutritional condition studies of these three species. Metabolic activity and resource utilization most likely differs dramatically among the three species. *Lepidonotothen larseni* may depend on long term transport and association with more pelagic waters for their optimal survivorship as evidenced by their higher condition in the axial current in Gerlache Strait. *Trematomus newnesi* is robust and appears to make horizontal migrations in the study area (Loeb 1992; Loeb et al. in press). Thus, its energy requirements would be higher than those of more passively drifting taxa. Onshore distribution of *T. lepidorhinus* larvae is limited (i.e., very few larvae collected in the bays), perhaps by mortality or behavior, but the present research does not address this issue. Larval condition for all of these species appears related to distribution and transport, but behavior and differing physiology must play a role.

Other contributing factors make it difficult to clearly link Antarctic larval fish condition and environmental factors. Maternal investment in the form of substantial larval yolk reserves coupled with prolonged resorption times (Kellermann 1990) enables the larvae to cope with extended periods of food shortage (Kock and Kellermann 1991). This, combined with relatively large size at hatching and exogenous feeding soon after, raise the likelihood that starvation represents a limited source of mortality for these larvae. Thus, nutritional condition may not adequately predict potential larval survivorship.

Maternal investment in the eggs and larvae may represent a source of variation in larval condition that was not tested in the present study. Following the work of Kellermann and Kock (1991), eggs of *L. larseni* are ca. 2.0 mm diameter, hatch length is ca. 7.0 mm, the gonadosomatic index (GSI) of adult females is ca. 12, and the potential fecundity is 1,851-7,070 eggs per female. Less information is known for the two other

species, the egg diameter of *T. newnesi*: is >2.5 mm and hatch length is ca. 9.0 mm. For *T. lepidorhinus* from the Weddell Sea, egg diameter is ≥2.6 mm, hatch lengths range from 8.7-11 mm, GSI >14, and fecundity ranges from 2,200-10,800 eggs per female. However, the smallest larvae recorded in our data ranged from 6.1-7.0 mm notochord lengths. From these data, it can be hypothesized that *L. larseni* invest greater maternal reserves in their larvae than do *T. lepidorhinus* females. However, *T. lepidorhinus* larvae have the largest yolk reserves standardized for body length of these three species (Laman and Loeb 1994). It cannot be determined from the present research what influence maternal investment has over subsequent larval condition.

Similar to results from Cowen et al. (1993), it appears from the present study that the factors having the greatest influence on larval condition and, potentially, survivorship are spawning location, larval dispersal and distribution, and possibly species-specific larval behavioral differences. Other researchers have proposed linkage between distribution patterns of Antarctic ichthyoplankton and broad patterns of regional hydrography (Kellermann and Kock 1988; Loeb 1991) and Huntley and Niiler (1995) propose that the most important hydrographic feature determining zooplankton population dynamics in the Southern Ocean is horizontal advection. For the species examined here, larval distribution reflects the gross hydrography of the region (Loeb 1991, 1993; Laman and Loeb 1995; Loeb et al. in press) and nutritional condition is positively correlated with larval density. Thus, the most important factors in determining larval condition may be the spawning location in relation to horizontal advection and behavioral adaptations which maximize transport or retention in suitable nursery areas.

If food were not a limiting resource in Antarctic larval fish communities due to factors such as an adequate supply, resource partitioning, or large yolk reserves, then measures of larval condition would reflect factors other than nutrition affecting potential survivorship. Thus, if condition indices utilized here do not reflect food availability and

assimilation, then they might reflect a direct link between larval condition and the physical/biotic environment. However, results from the present research showed only a single case where there appeared to be a direct effect on larval condition of a simple hydrographic feature chosen (i.e., temperature effects on *T. newnesi* yolk utilization). This could indicate that factors other than nutrition and/or the simple hydrography are affecting larval condition or that we were unable to detect the linkage that truly existed. The most likely explanation is that the data selected for analyses (i.e., morphometric condition factors and simple hydrographic features) were inadequate to the task of resolving the true condition of the larvae and how it related to their behavior, metabolism, growth rates, and environment.

As suggested by Sieg (1993) and Cone (1989), the use of a length-based condition factor is not adequate to accurately describe the true condition of larval fishes. These flaws were partially mitigated in the present study by including the related condition measures *SSA* and *F*. There may also be some difficulties in estimating condition from length/weight relationships if larval growth rates vary within the early life stages. Any future studies of the condition of larval Antarctic fishes would benefit from the use of either RNA/DNA ratio comparisons or histological examination of internal organ development. Both of these techniques were precluded in the present study by the fact that the specimens had been preserved in formalin for an extended period of time. If morphometric condition measures are employed, then *SSA* and *F* are more informative indices than the traditional length-based relative condition factor.

CONCLUSIONS

Each of the three species examined above exhibited evidence of growth and length-related differences over the advancing spring season in Gerlache Strait: yolk reserves were smaller; the proportion of yolk-sac larvae decreased; gut fullness and feeding incidence were higher; condition factors increased. However, samples from Marguerite Bay in late

spring presented some exceptions to these generalities. Nearly all of the *L. larseni*, *T. newnesi* and *T. lepidorhinus* larvae collected in this region were in the yolk-sac phase. This strongly suggests that better feeding conditions existed for larvae here and that less than optimal feeding conditions exist in the Gerlache Strait region.

Comparing the two seasons, it is apparent that the center of larval *T. lepidorhinus* abundance was located in Marguerite Bay and it can be hypothesized that this is a major source area. The low abundance of *L. larseni* and *T. newnesi* larvae in Marguerite Bay likely reflects their adult distributions which are in lower latitudes. Both of these conclusions support the general indication that these larvae had the highest condition where they were most abundant.

Significant associations of environmental factors with *L. larseni* and *T. lepidorhinus* coincided with their vertical distribution patterns and probably were not functional relationships. Only *T. newnesi* clearly demonstrated the effects of environmental forcing. In the center of their vertical distribution, larval condition and gut fullness were relatively high and similar in the regions compared, but yolk reserve sizes were markedly depressed at station "A". This accelerated yolk utilization coincided with the intrusion of an anomalously high temperature, low salinity water mass into the 0-15 m stratum during early spring. The high temperature could have increased metabolic and respiratory activity or enhanced enzymatic activity and thereby yolk utilization. Low salinity water could also effect larval buoyancy and impart an increased energetic cost to larvae trying to maintain their vertical position.

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TABLES

Table 1. Young fish abundance and composition in the RACER II samples collected in Gerlache Strait, October-November 1989. Presence is the percent of the total 23 stations at which each species was collected (modified from Loeb 1993).

Species	Mean No./10m^2	Percent	Total No.	Presence (%)
Larvae:	10.74	57.63	538	100.0
Lepidonotothen larseni	3.72	19.97	599	82.6
Trematomus newnesi	1.25	6.69	242	65.2
Electronaantarctica	0.89	4.77	19	56.5
Bathylagus sp(p).	0.65	3.51	44	52.2
Chionodraco rastropspinosus	0.63	3.36	34	47.8
Bathydraconid #1	0.23	1.24	7	26.1
Champsocephalus gunnari	0.16	0.88	9	17.4
Lepidonotothen nudifrons	0.12	0.66	10	26.1
Racovitzia glacialis	0.07	0.37	2	13.0
Artedidraco skottsbergi	0.07	0.35	21	26.1
Gobionotothen gibberifrons	0.04	0.22	14	13.0
Chionobathyscus dewitti	0.03	0.14	6	4.3
Notolepis sp(p).	0.01	0.04	2	8.7
Harpagiferantarcticus	<0.01	0.04	2	8.7
Unidentified B	<0.01	0.02	1	4.3
Unidentified A	<0.01	<0.01	1	4.3
Unidentified C	<0.01	<0.01	1	4.3
Bathydraconid #2	<0.01	0.01	1	4.3
Juvenile *Pleuragrammaantarcticum*	0.01	0.05	1	4.3
Lepidonotothen kempi (juvenile)	0.01	0.04	1	4.3
Damaged/unidentified	0.33		23	
TOTAL	18.97		1578	
Number of stations			23	
Number of tows			103	

Table 2. Fish early life stages in the RACER III samples collected in a) Gerlache Strait and b) Marguerite Bay, 15 December 1991 - 03 January 1992. Larval fish diversity is total number of taxa collected and the average number of taxa per tow in each area. Presence is percent of total stations at which each taxon was collected (modified from Loeb 1994).

a) Gerlache Strait: 38 stations; 102 tows. Species	Mean No./10m²	Percent	Total No.	Presence (%)
Larvae:				
Trematomus lepidorhinus	5.23	45.51	344	86.8
Lepidonotothen larseni	4.62	40.17	252	94.7
Chionodraco rastrospinosus	0.43	3.76	41	52.6
Gobionotothen gibberifrons	0.40	3.47	74	34.2
Bathylagus sp(p).	0.25	2.17	10	21.1
Notolepis coatsi	0.16	1.41	9	21.1
Trematomus newnesi	0.13	1.09	15	31.6
Electronaantarctica	0.09	0.76	5	13.2
Notolepis annulata	0.04	0.39	2	5.3
Artedidraco skottsbergi	0.03	0.29	6	10.5
Lepidonotothen nudifrons	0.03	0.28	2	5.3
Bathydraconidae	0.02	0.21	1	2.6
Artedidraco sp. A	0.02	0.18	2	5.3
Champsocephalus gunnari	0.02	0.17	2	5.3
Cryodraco antarcticus	0.01	0.12	1	2.6
Notothenia neglecta	<0.01	<0.01	1	2.6
Pleuragramma antarcticum	—	—	—	—
Prionodraco evansii	—	—	—	—
Damaged/umidentified	0.16		11	
Total Larvae	11.66		778	100.0
Diversity (No. of taxa)	2.20		16	
Juveniles:				
Pleuragramma antarcticum	—	—	—	—
Trematomus scotti	—	—	—	—
Paraliparid	—	—	—	—

(Table 2 continued)

b) Margerurite Bay: 13 stations; 13 tows. Species	Mean No./10m^2	Percent	Total No.	Presence (%)
Larvae:				
Trematomus lepidorhinus	46.65	45.82	850	100.0
Lepidonotothen larseni	0.48	0.47	4	15.4
Chionodraco rastrospinosus	0.03	0.03	1	7.7
Gobionotothen gibberifrons	0.10	0.10	2	7.7
Bathylagus sp(p).	—	—	—	—
Notolepis coatsi	—	—	—	—
Trematomus newnesi	1.36	1.34	26	61.5
Electronaantarctica	0.10	0.09	1	7.7
Notolepis annulata	0.13	0.13	1	7.7
Artedidraco skottsbergi	0.06	0.06	2	15.4
Lepidonotothen nudifrons	—	—	—	—
Bathydraconidae	—	—	—	—
Artedidraco sp. A	0.36	0.35	6	30.8
Champsocephalus gunnari	—	—	—	—
Cryodraco antarcticus	—	—	—	—
Notothenia neglecta	—	—	—	—
Pleuragramma antarcticum	52.48	51.55	1491	30.8
Prionodraco evansii	0.06	0.06	1	7.7
Damaged/umidentified	0.36		5	
Total Larvae	102.17		2390	100.0
Diversity (No. of taxa)	2.90		11	
Juveniles:				
Pleuragramma antarcticum	0.89		4	30.8
Trematomus scotti	0.12		1	7.7
Paraliparid	0.65		3	23.1

FIGURES

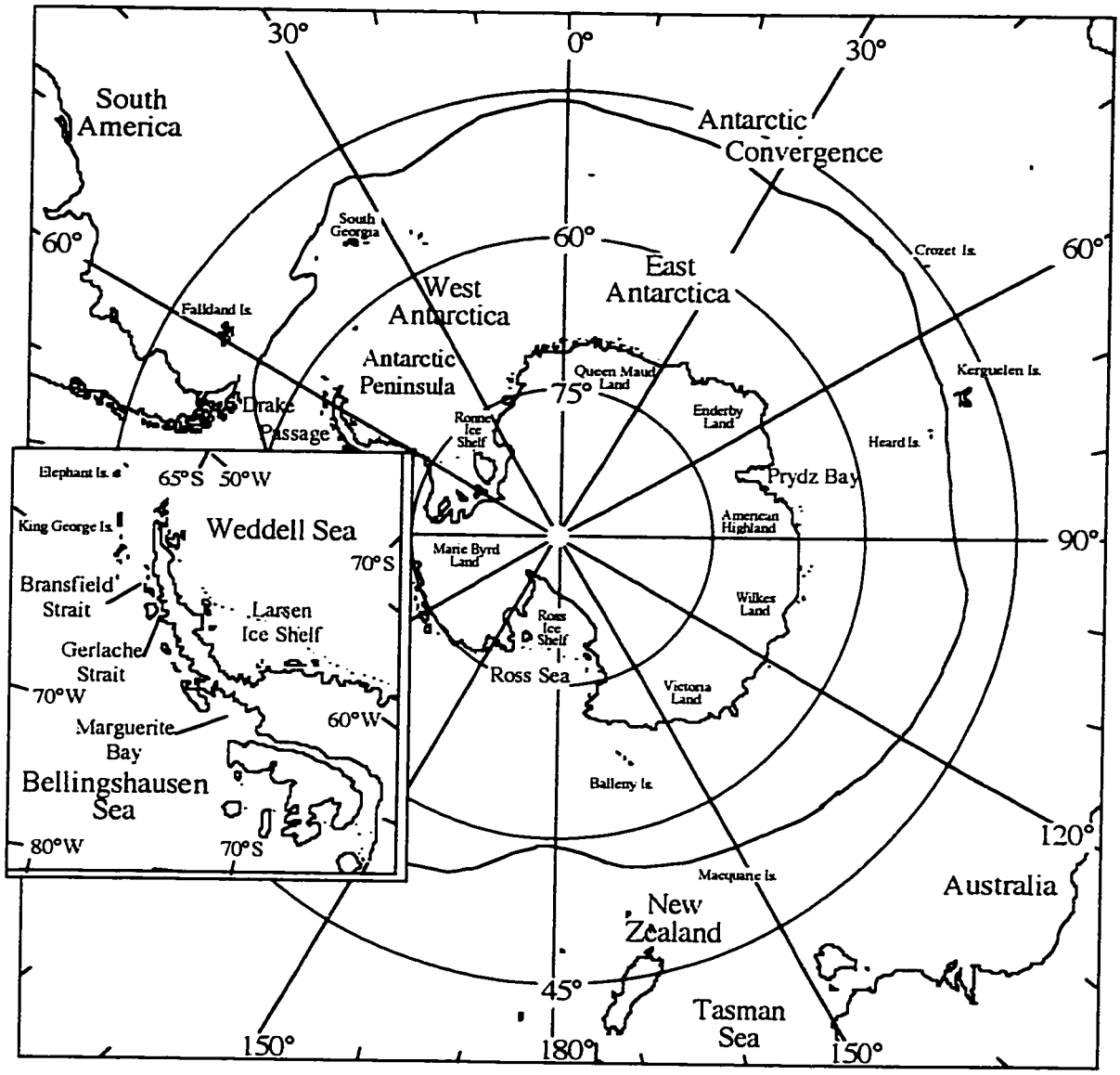


Figure 1. Map of Antarctica with study area highlighted in inset.

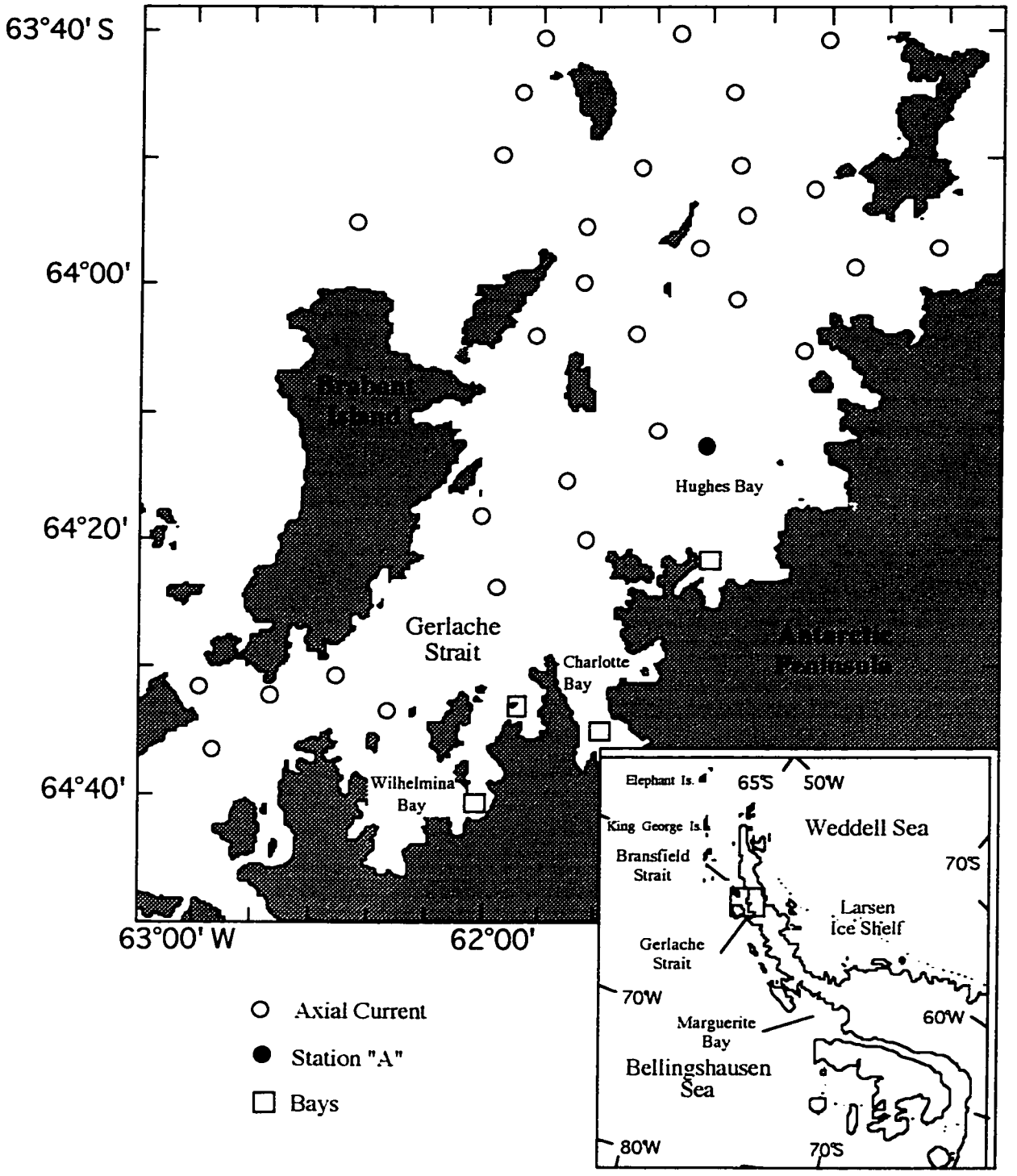


Figure 2. RACER II: Early spring 1989 Gerlache Strait, Antarctica sampling grid; axial current and bays constitute "F"-series sampling grid, station "A" is the time series sampling location.

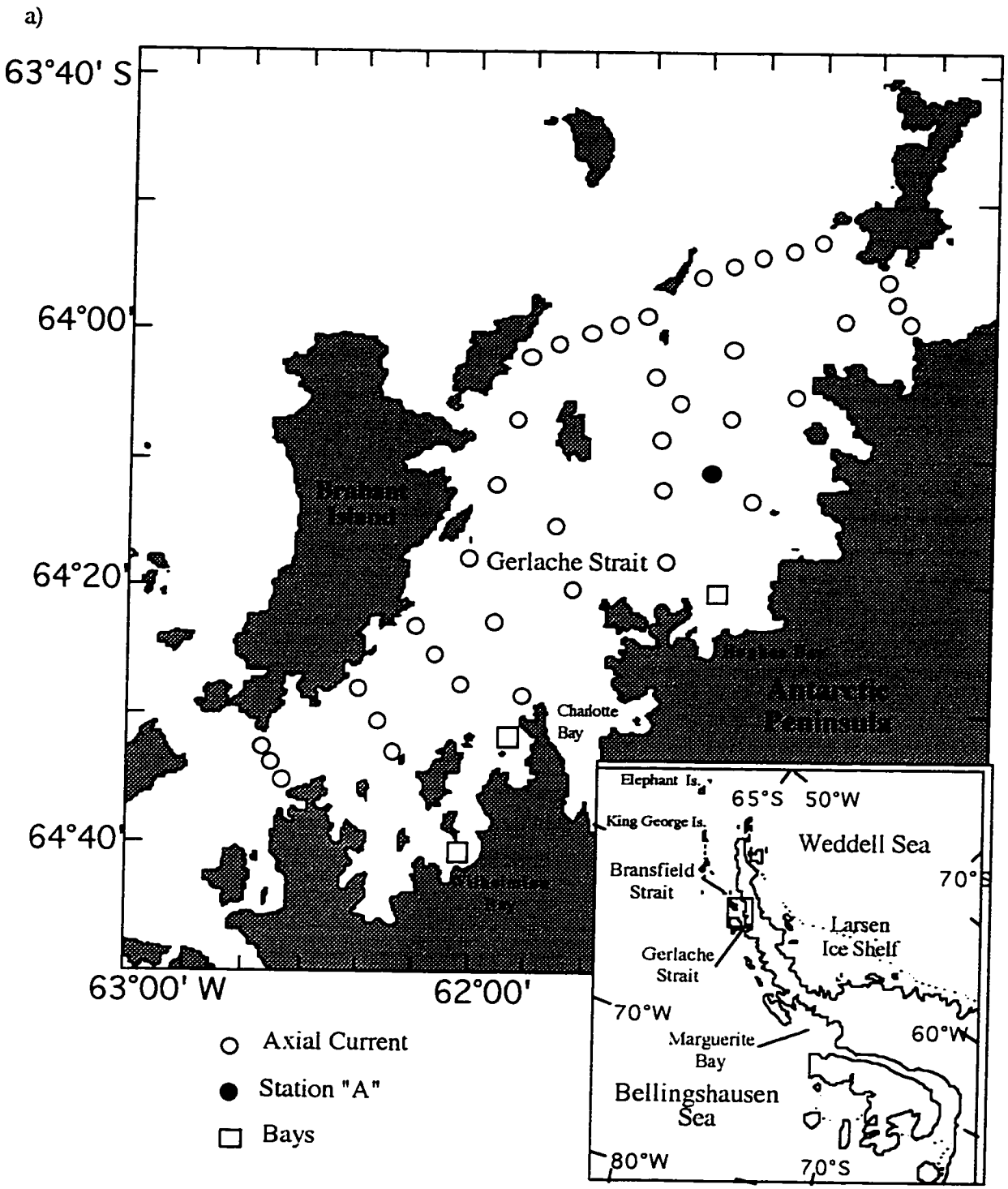
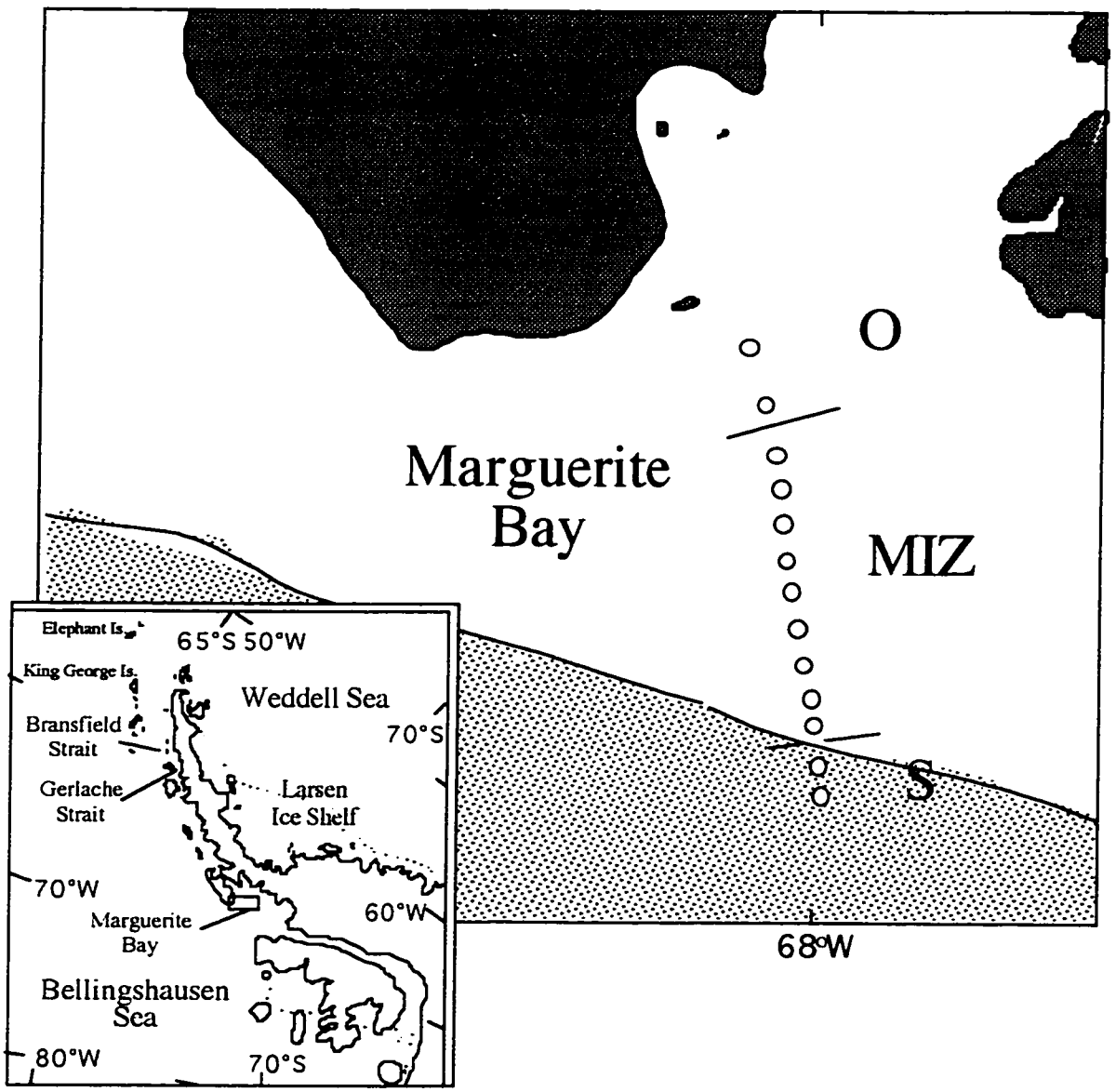


Figure 3. RACER III: Late spring 1991-92 sampling grids: a) Gerlache Strait (axial current, bays, and station "A"); b) Marguerite Bay Ice Edge (sea-ice denoted by stippled area; O=open ocean, MIZ=marginal ice zone, and S=sea-ice).

Figure 3 continued

b)



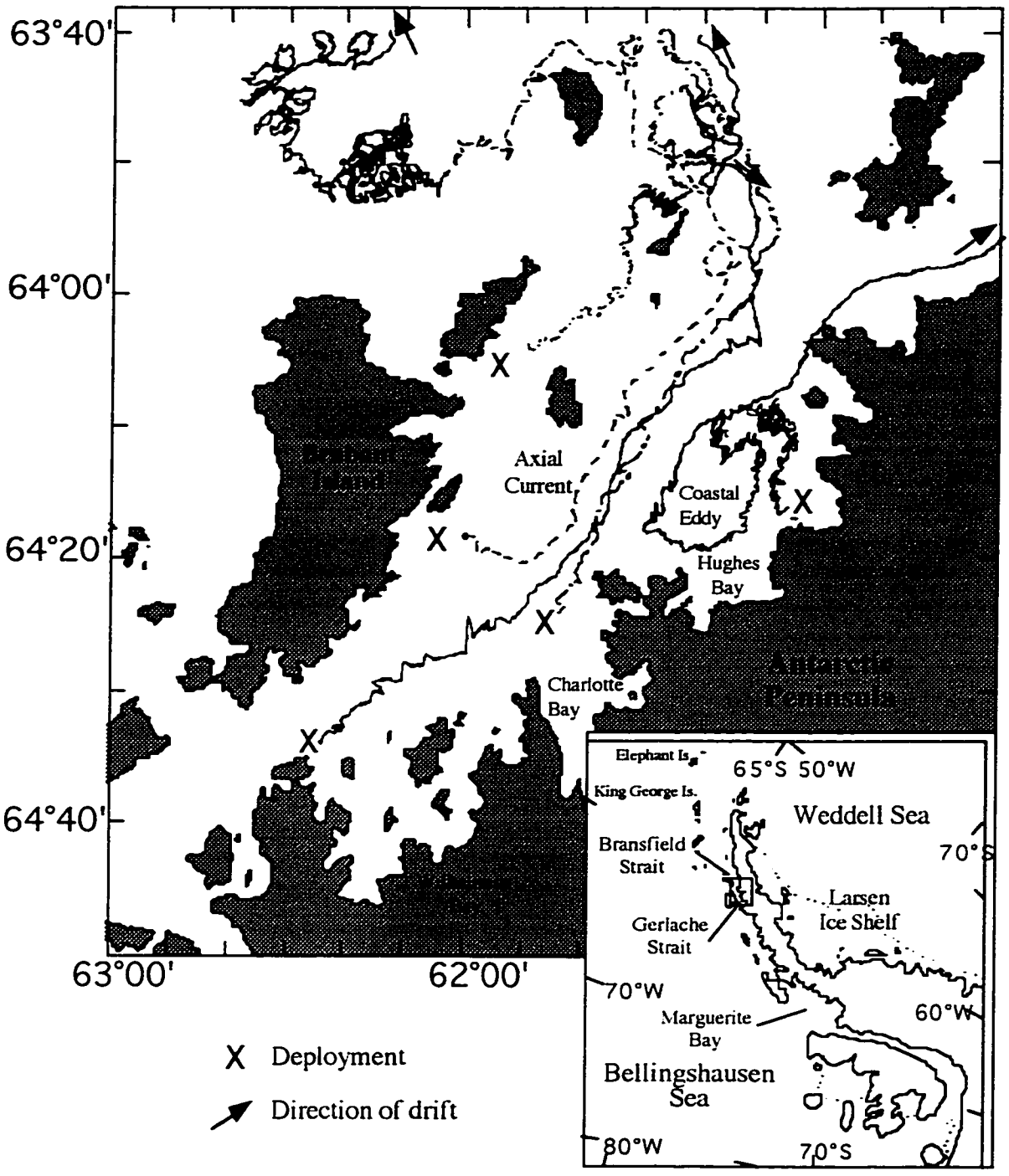


Figure 4. RACER study area with tracks of five Tristar drifters launched during the early spring 1989 (X's indicate deployment sites, arrows indicate last recorded direction of travel) sampling period showing three hydrographic regions of potentially differing larval fish feeding conditions: a coastal eddy; bays (Wilhelmina, Charlotte, and Hughes Bays); and an axial current (modified from Lopez *et al.* 1993).

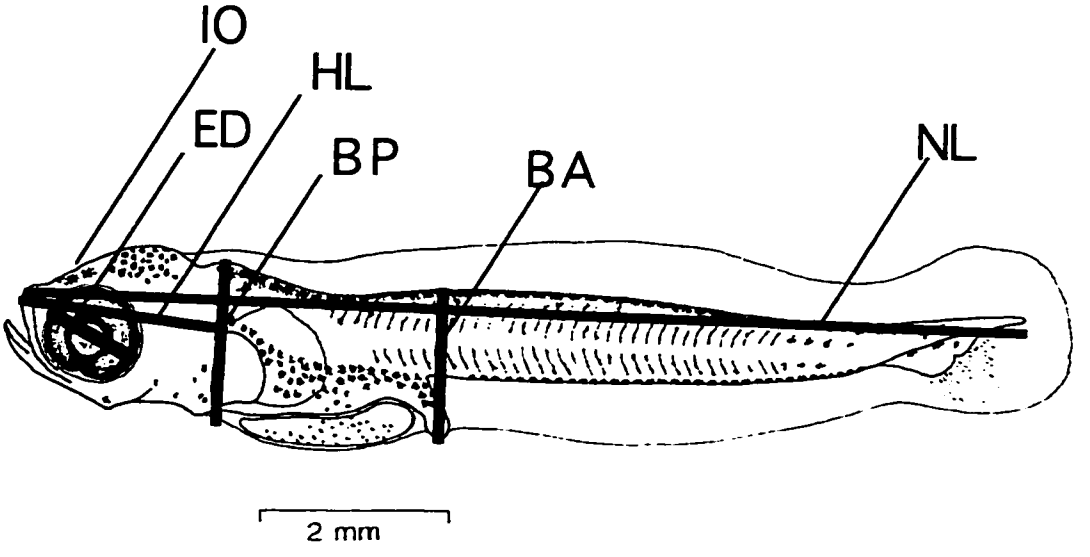


Figure 5. Measurements taken on larvae for condition factor analyses. *Trematomus newnesi* larva depicted here was modified from Kellermann (1989).

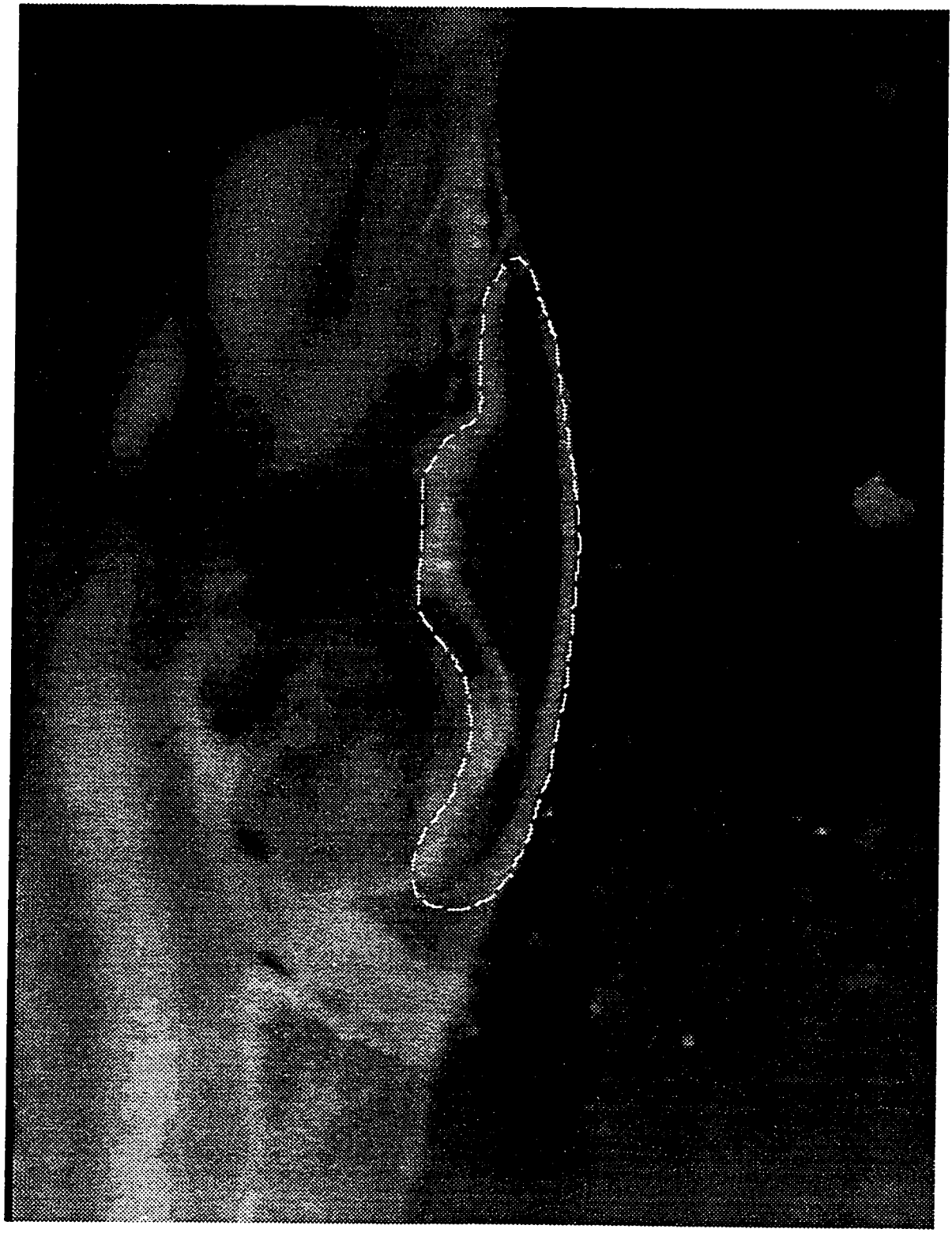


Figure 6. Digitized image of the yolk-sac (outlined) of *Trematomus newnesi* larva.

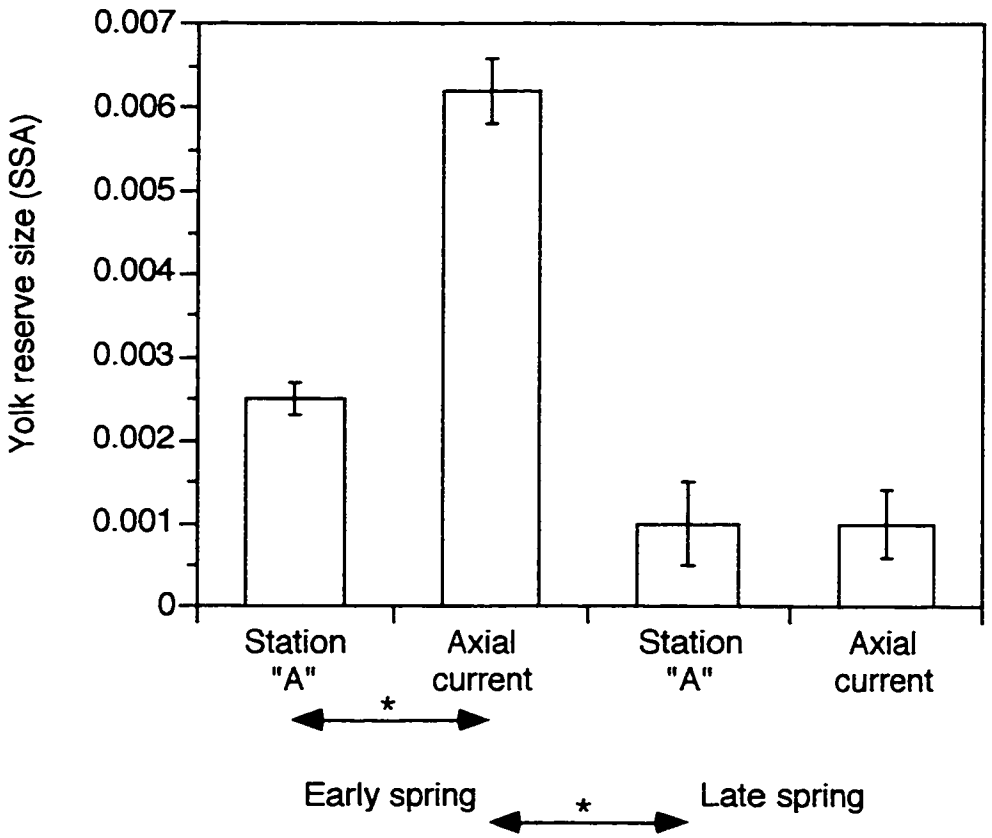


Figure 7. Comparison of mean yolk reserve sizes (*SSA*) between Station "A" and the Axial Current and between early and late spring for *Lepidonotothen larseni* larvae (asterisks and arrows indicate significant differences).

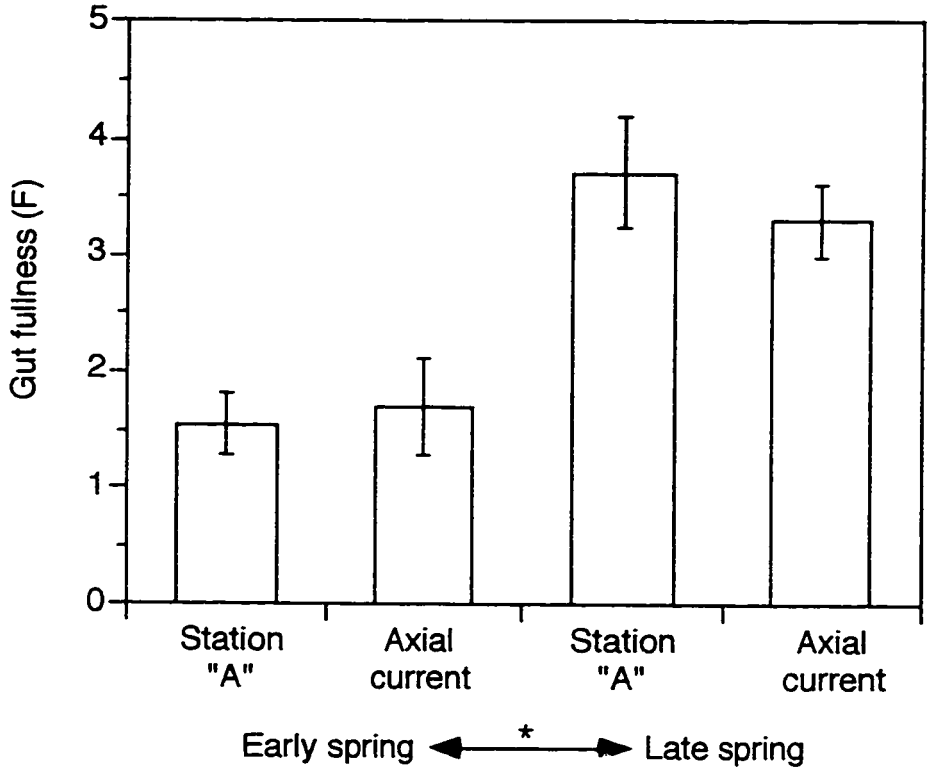


Figure 8. Comparison of mean gut fullness (*F*) between Station "A" and the Axial Current and between early and late spring for *Lepidonotothen larseni* larvae (asterisc and arrow indicate significant difference).

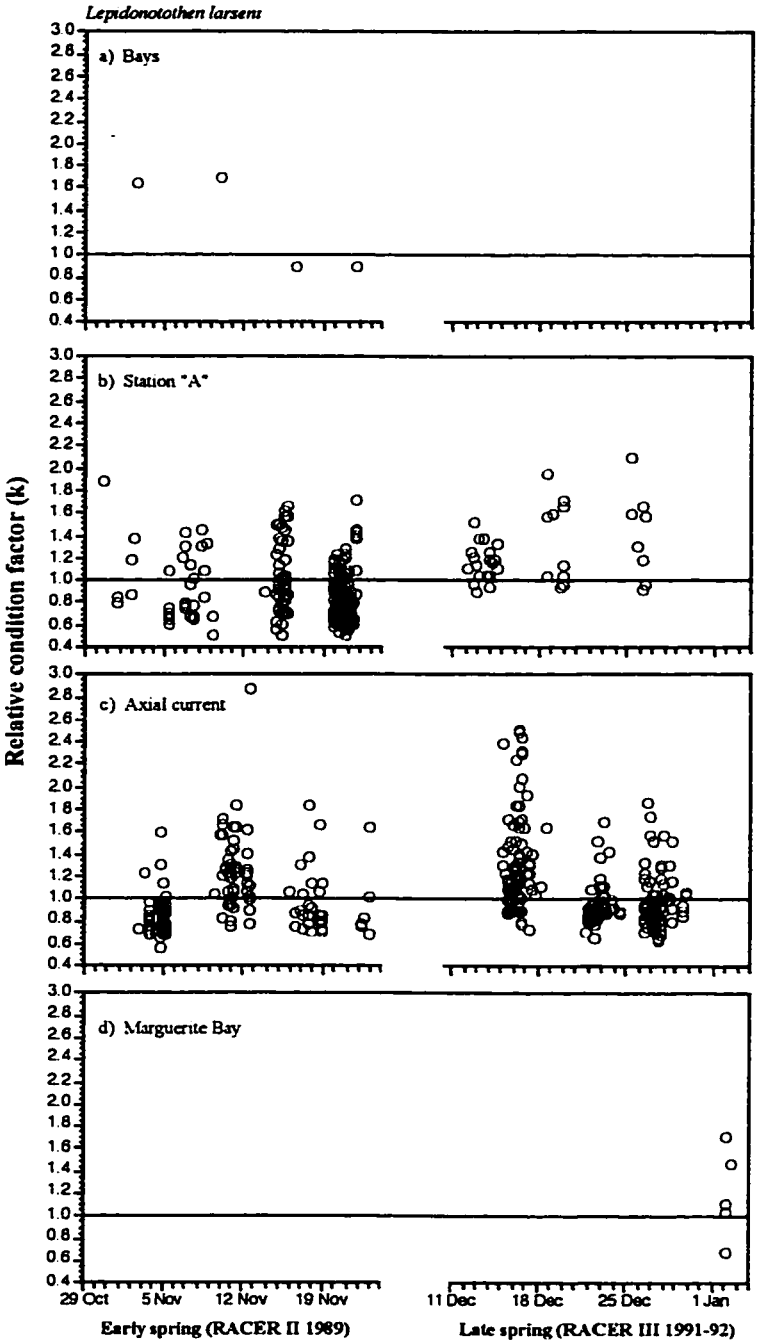


Figure 9. Relative condition factors (k) of *Lepidonotothen larseni* larvae collected during early (RACER II) and late (RACER III) spring in a) Bays, b) at Station "A", c) the Axial Current, and d) Marguerite Bay; k=1.0 is the ideal predicted condition based on the empirical length/weight relationship.

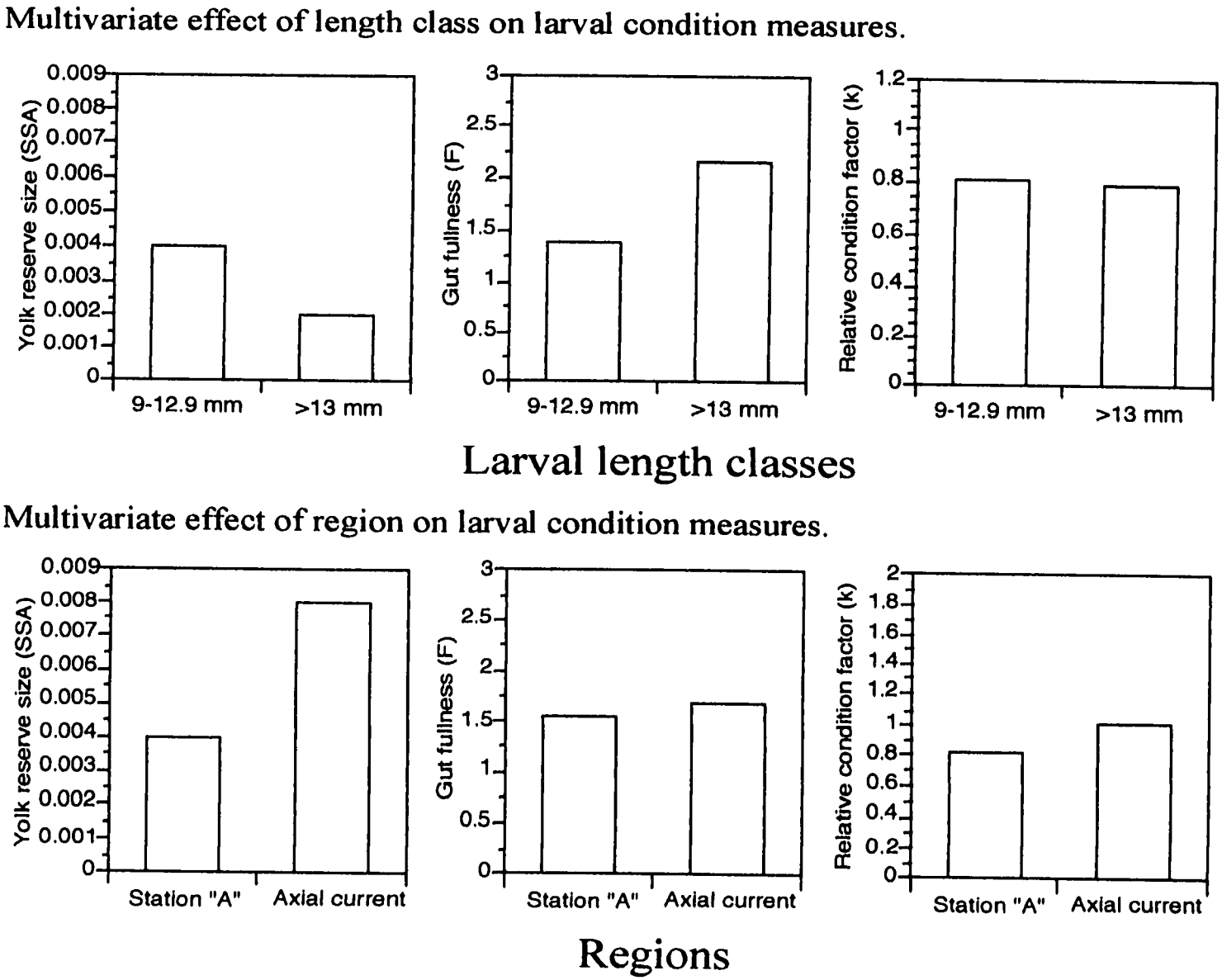


Figure 10. Significant multivariate effects of a) larval length and b) regions on larval condition of *Lepidomotothen larseni* collected during early spring.

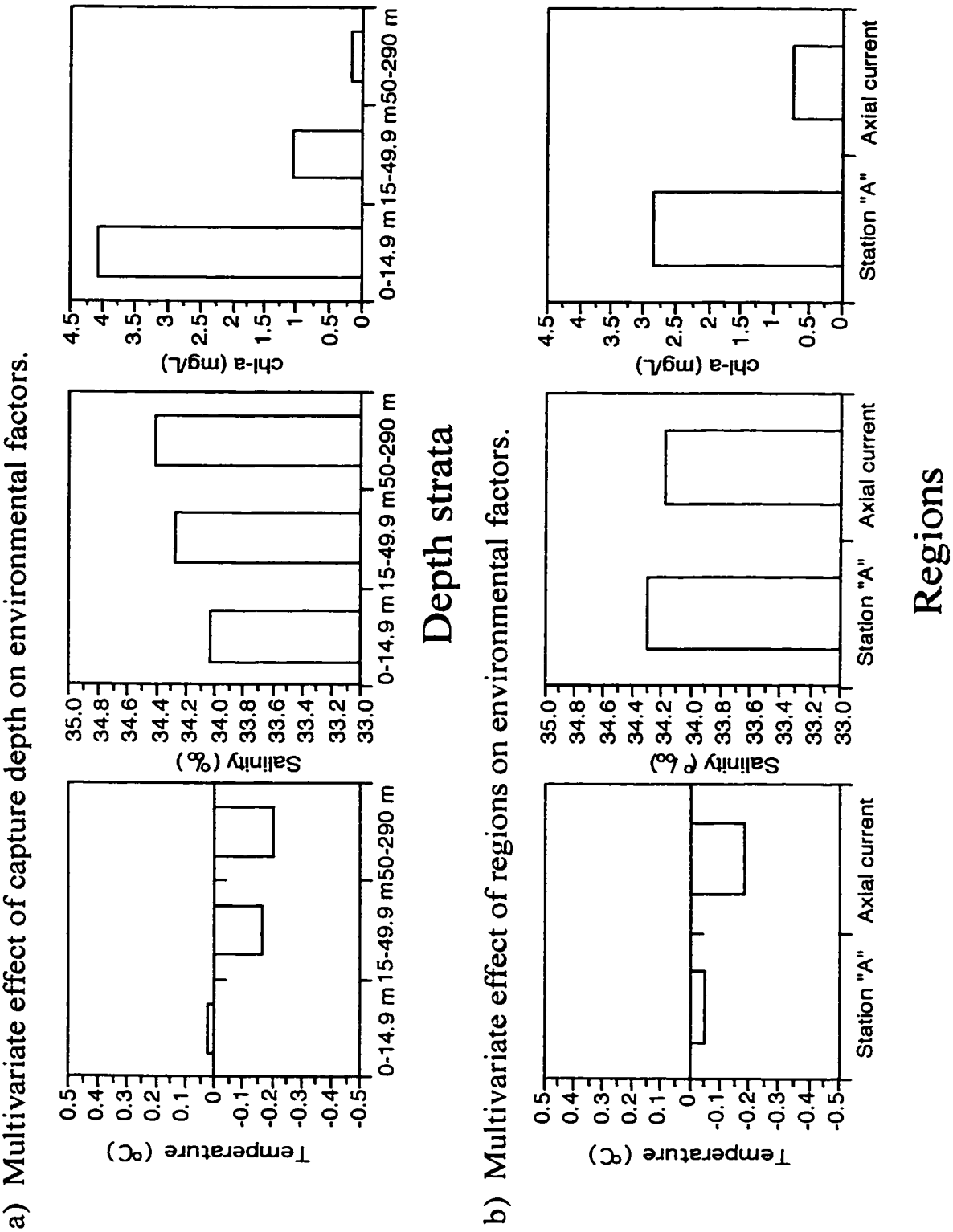


Figure 11. Significant multivariate effects of a) capture depth and b) regions on environmental factors associated with *Lepidonotothen larseni* larvae collected during early spring.

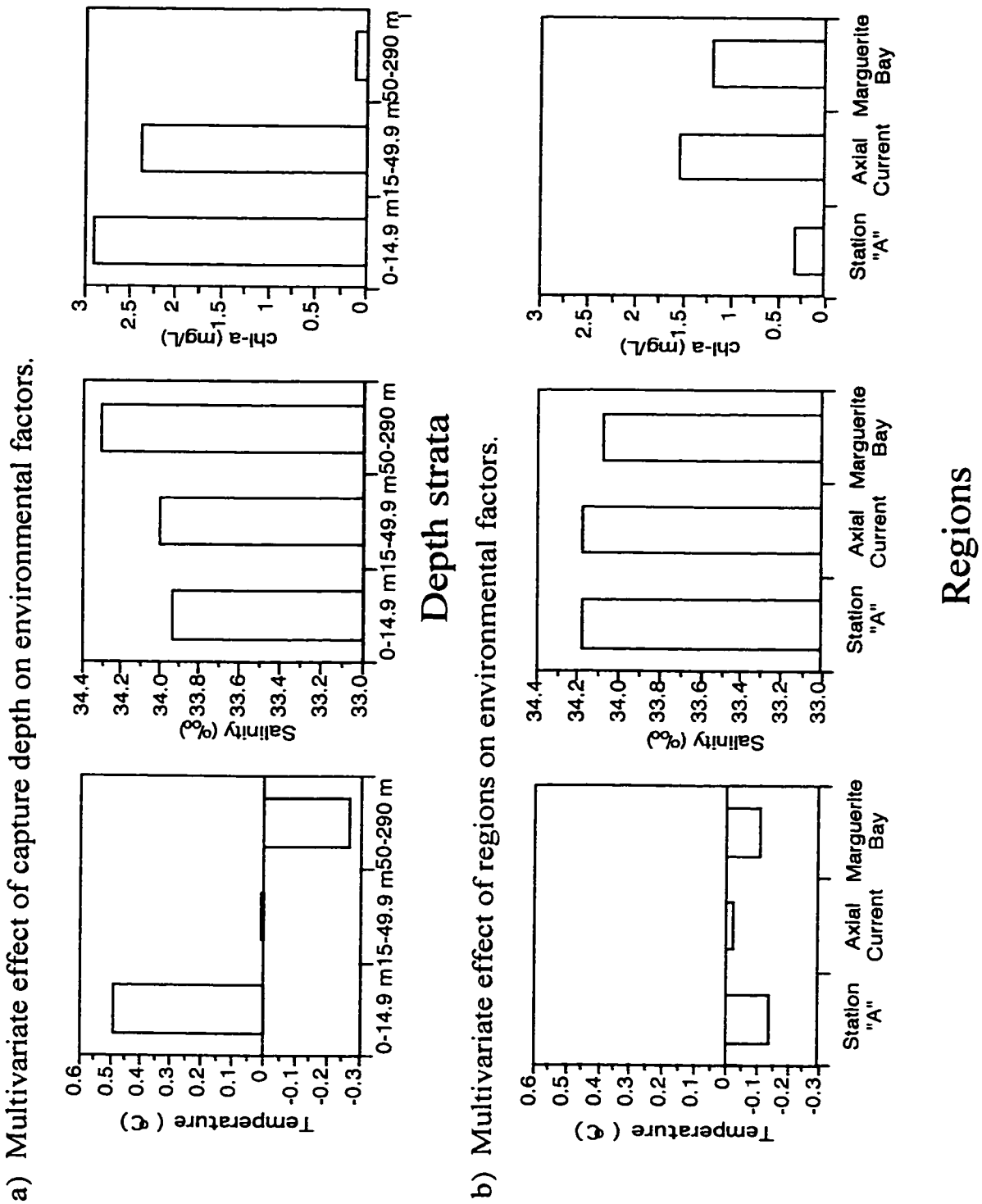


Figure 12. Significant multivariate effects of a) capture depth and b) regions on environmental factors for *Lepidonotothen larseni* larvae collected during late spring.

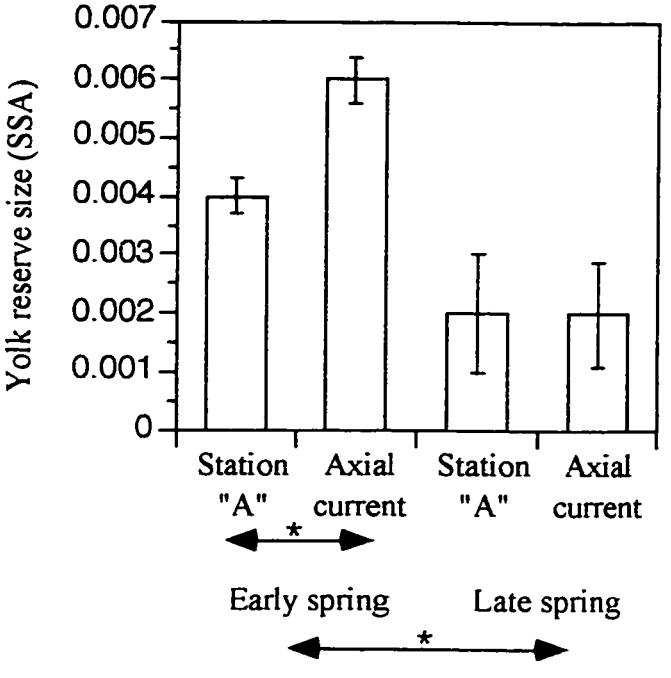


Figure 13. Comparison of mean yolk reserve sizes (*SSA*) between Station "A" and the Axial Current and between early and late spring for *Trematomus newnesi* larvae (asterisks and arrows indicate significant differences).

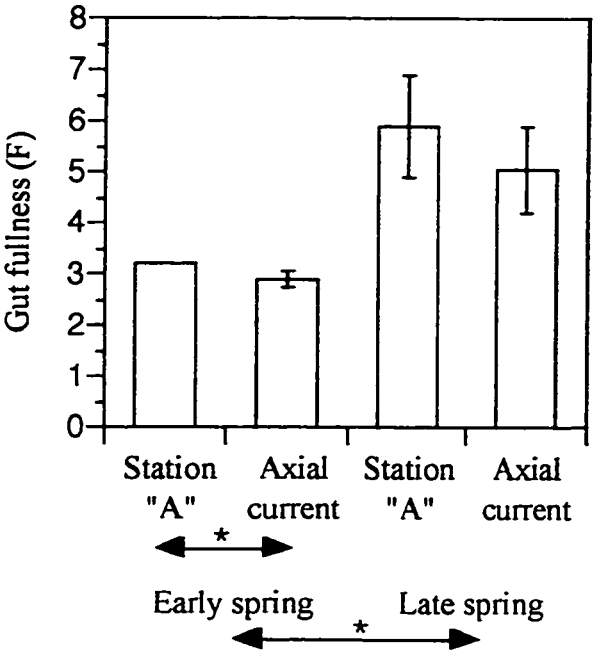


Figure 14. Comparison of mean gut fullness (*F*) between Station "A" and the Axial Current and between early and late spring for *Trematomus newnesi* larvae (asterisks and arrows indicate significant differences).

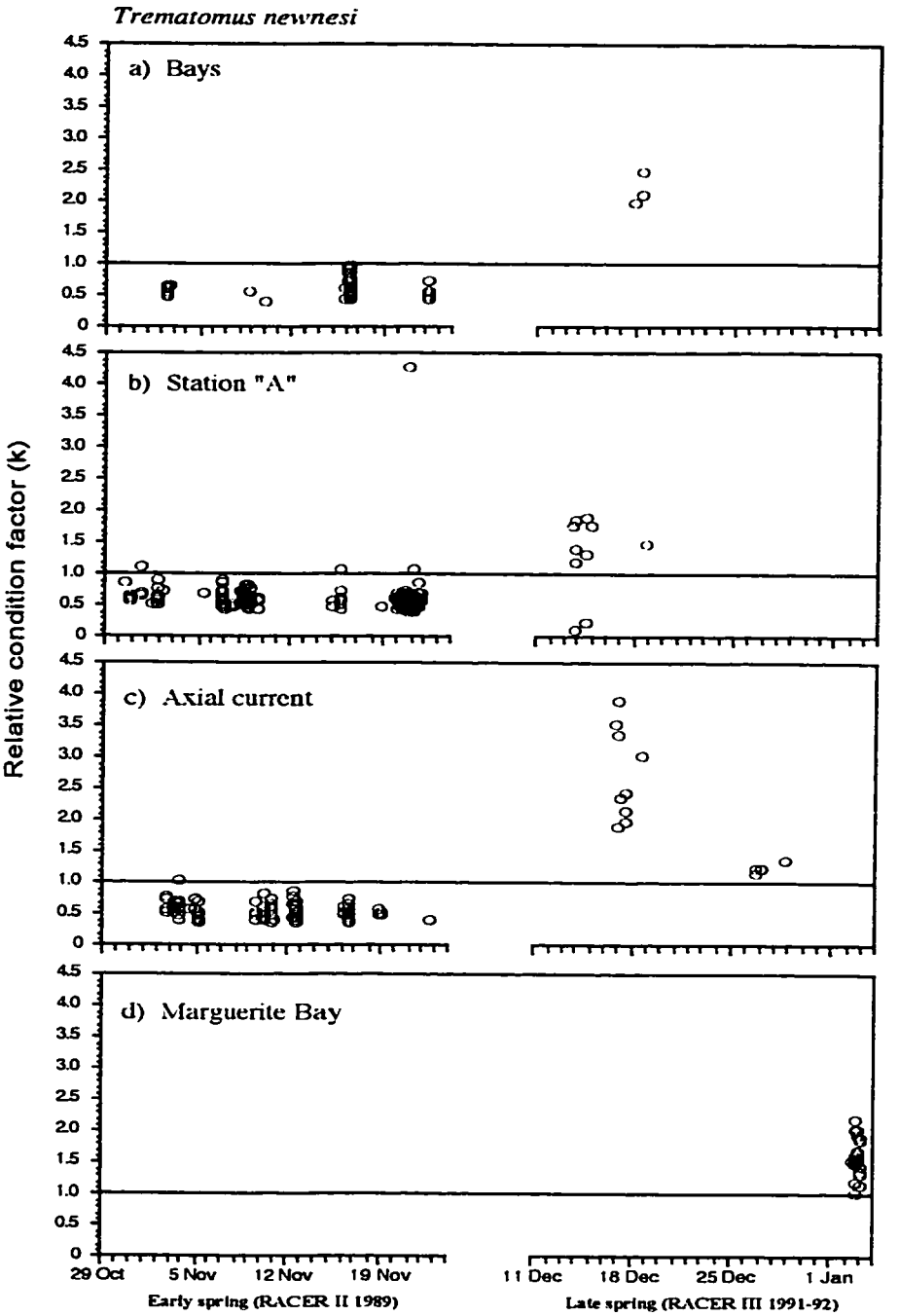


Figure 15. Relative condition factors (k) of *Trematomus newnesi* larvae collected during early (RACER II) and late (RACER III) spring in a) Bays, b) at Station "A", c) the Axial Current, and d) Marguerite Bay; k=1.0 is the ideal predicted condition based on the empirical length/weight relationship.

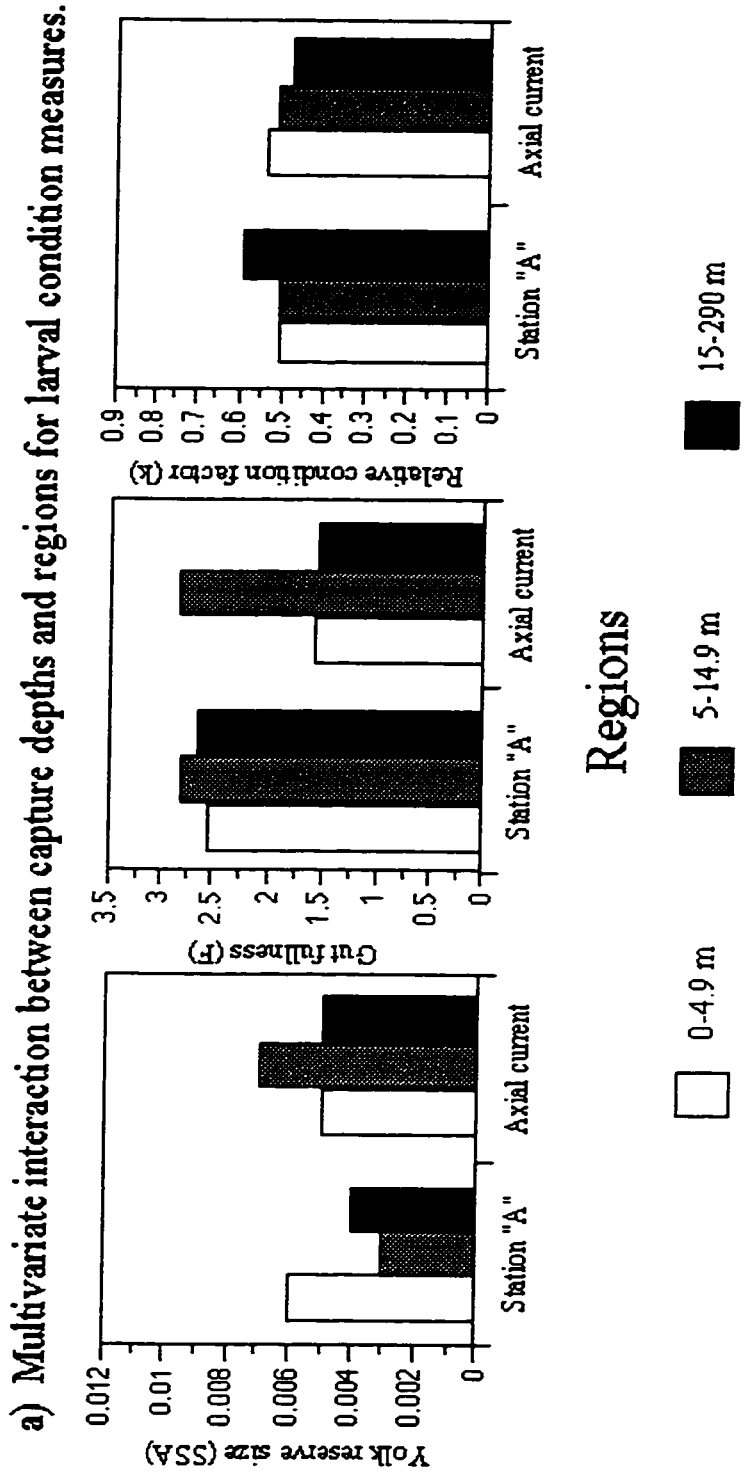


Figure 16. Significant multivariate interaction between a) capture depth & regions for measures of condition (*SSA*, *F*, and *k*) of *Trematomus newnesi* larvae collected during early spring.

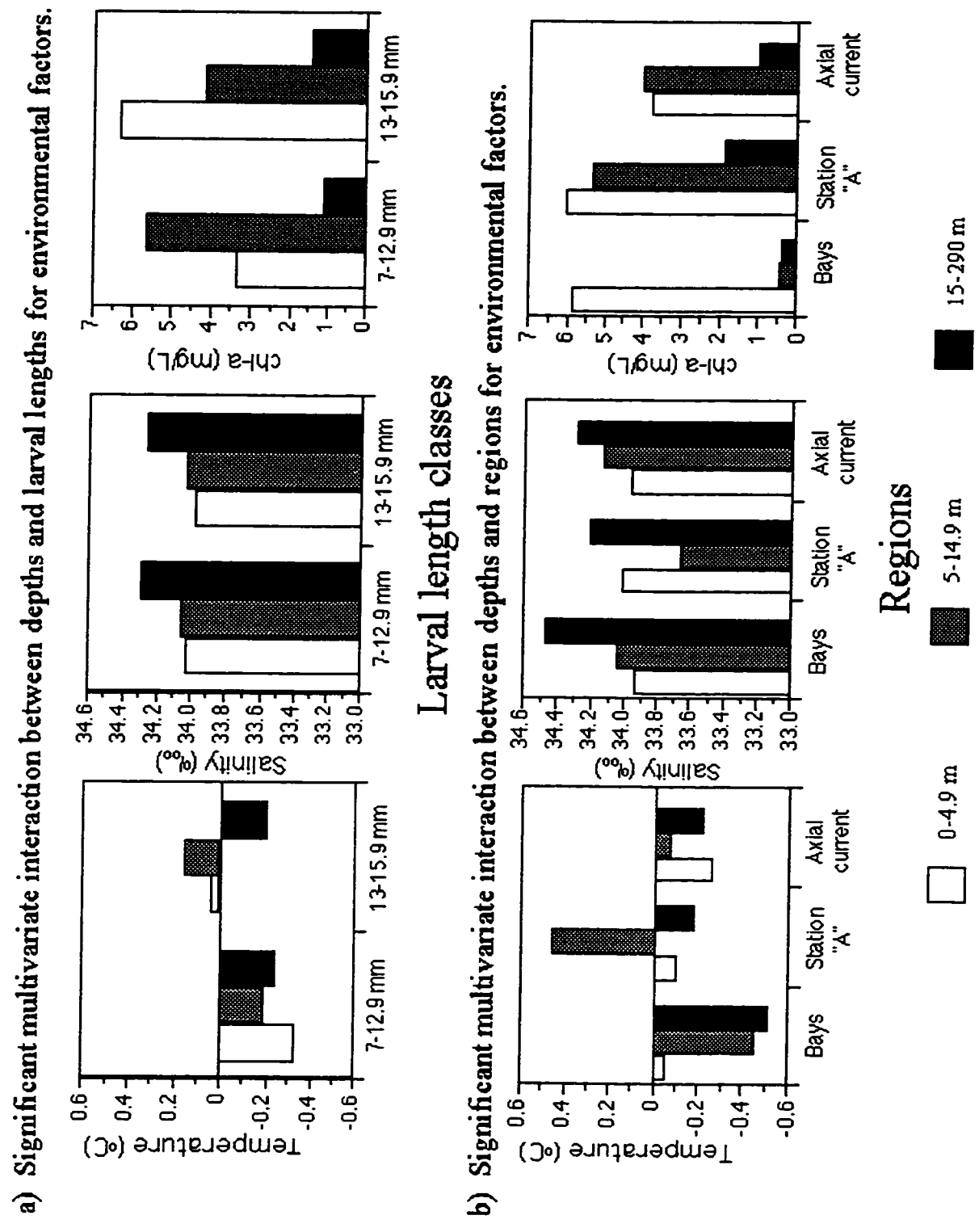
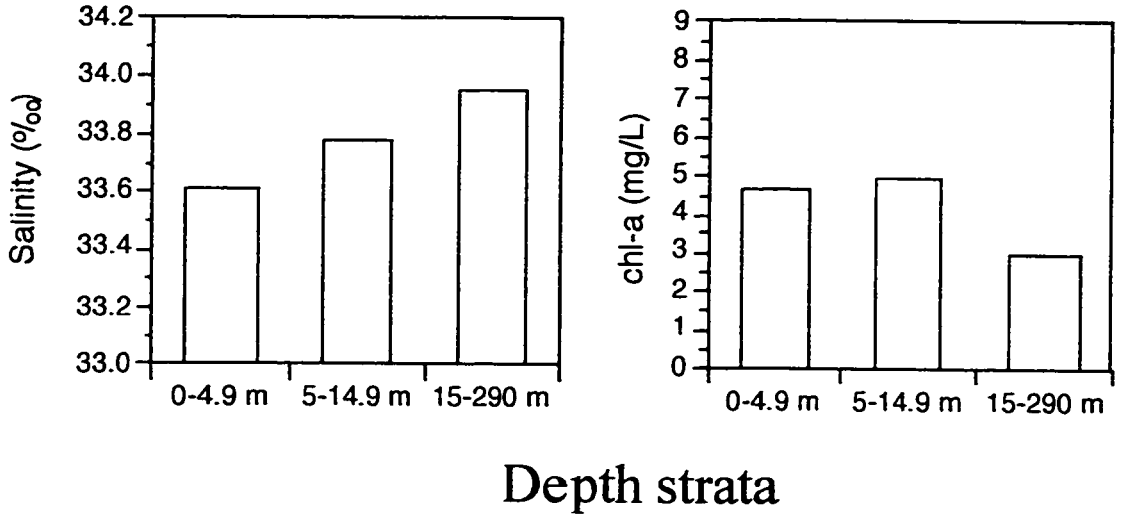


Figure 17. Significant multivariates effects of a) capture depth & larval lengths and b) capture depth & regions on environmental factors associated with *Trematomus newnesi* larvae collected in early spring.

a) Significant multivariate effect of depths on environmental factors.



b) Significant multivariate effect of regions on environmental factors.

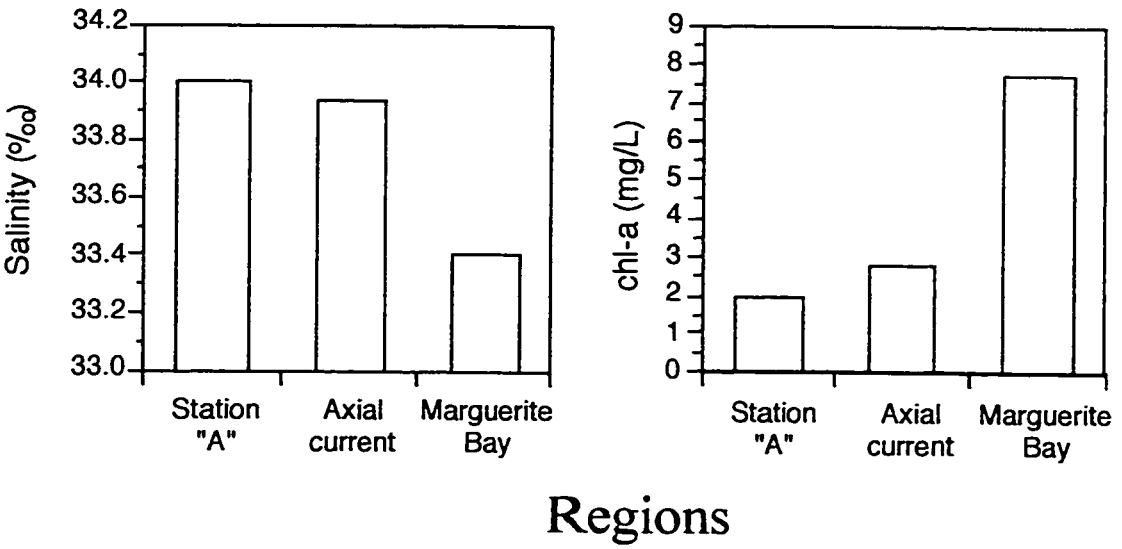


Figure 18. Significant multivariate effects of a) catpure depth and b) regions on environmental factors (salinity in parts per thousand; chlorophyll-*a* concentration in milligrams per liter) associated with *Trematomus newnesi* larvae collected during late spring.

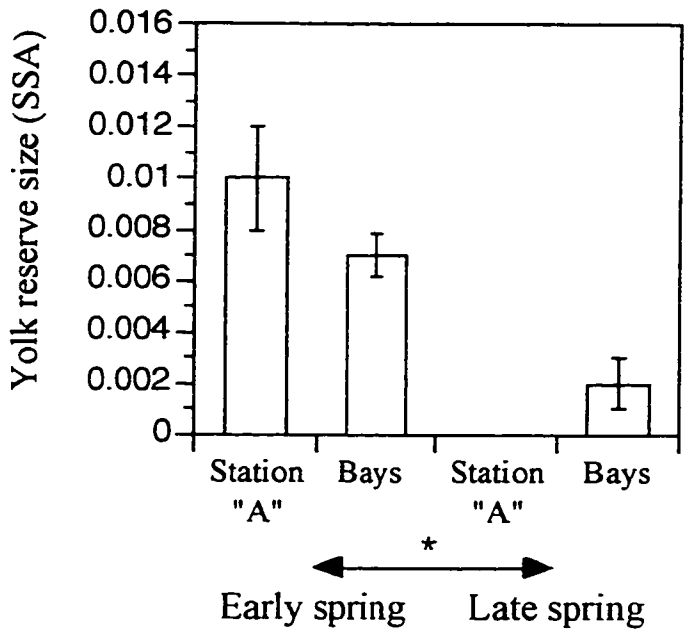


Figure 19. Comparison of mean yolk reserve size at station "A" with bays for *Trematomus lepidorhinus* larvae; * indicates statistically significant difference between early and late spring samples.

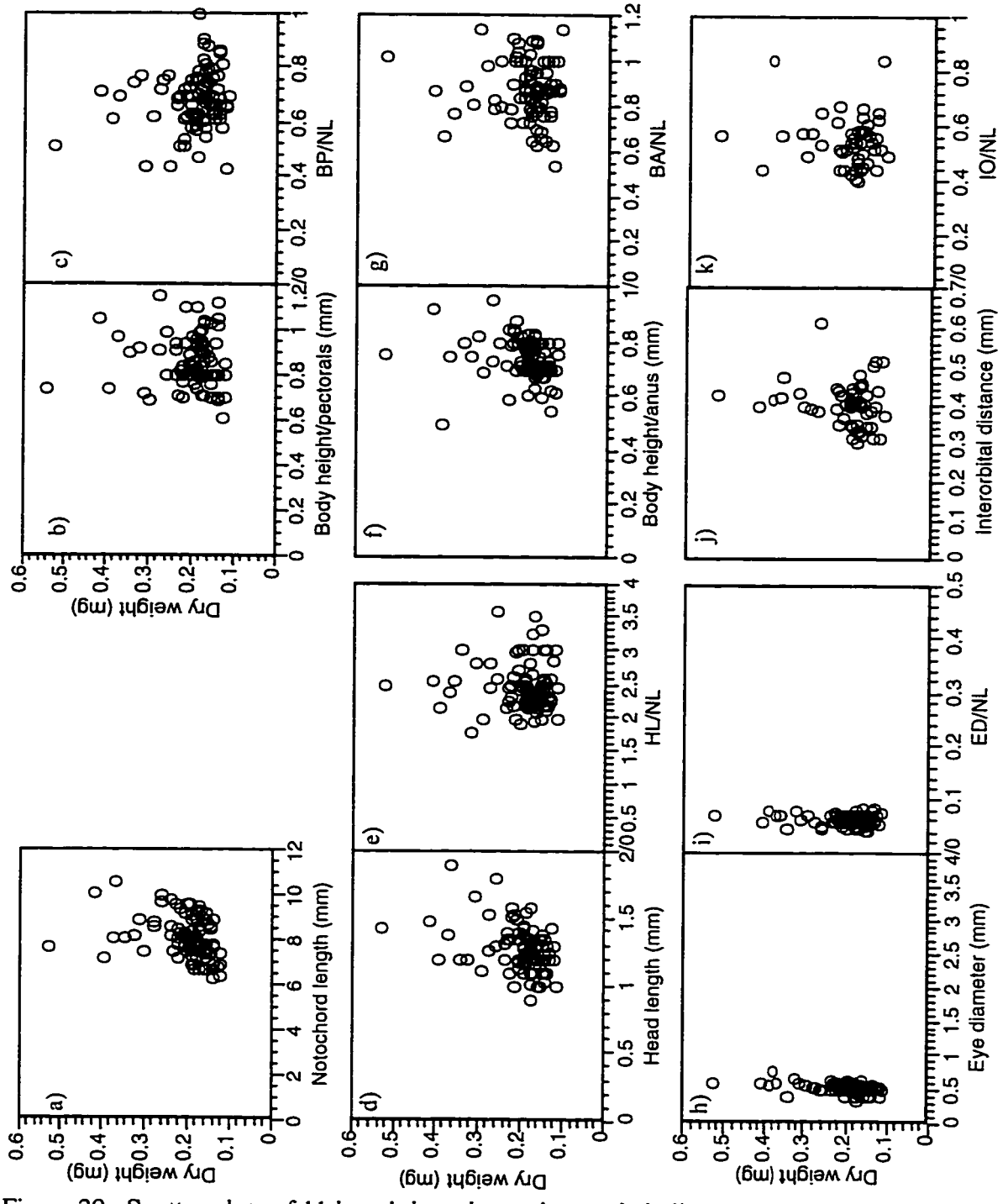


Figure 20. Scatter plots of 11 length-based morphometric indices measured on *Trematomus lepidorhinus* larvae to predict dry weight (*DW*): a) *DW* vs. notochord length (*NL*); b) *DW* vs. body height at the pectorals (*BP*); c) *DW* vs. *BP/NL*; d) *DW* vs. head length (*HL*); e) *DW* vs. *HL/NL*; f) *DW* vs. body height at the anus (*BA*); g) *DW* vs. *BA/NL*; h) *DW* vs. eye diameter (*ED*); i) *DW* vs. *ED/NL*; j) *DW* vs. interorbital distance (*IO*); k) *DW* vs. *IO/NL*.

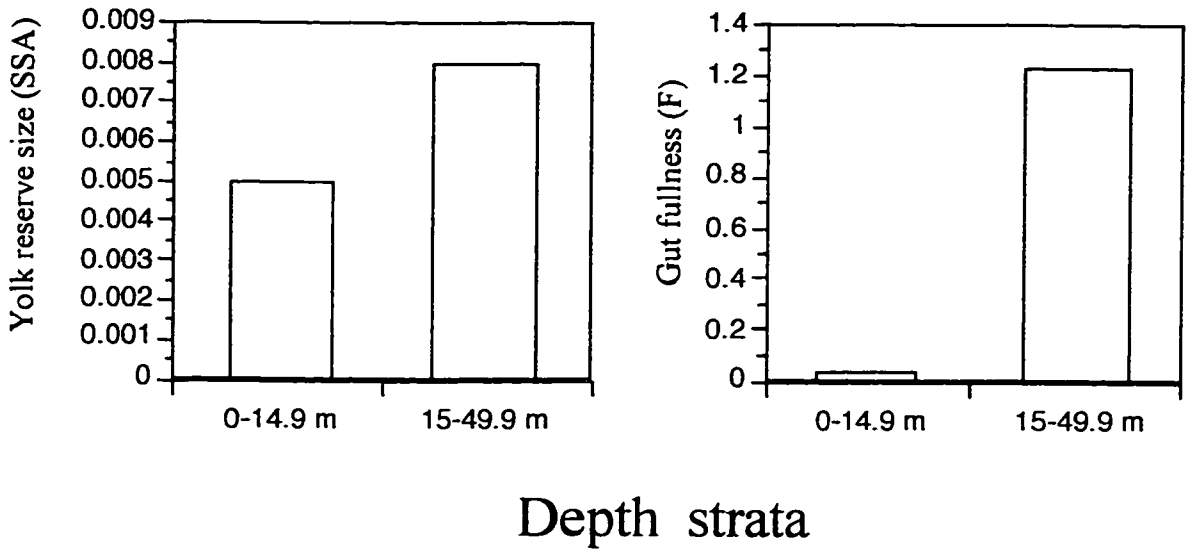


Figure 21. Significant multivariate effect of capture depth on condition (*SSA* and *F*) of larval *Trematomus lepidorhinus* collected during early spring.

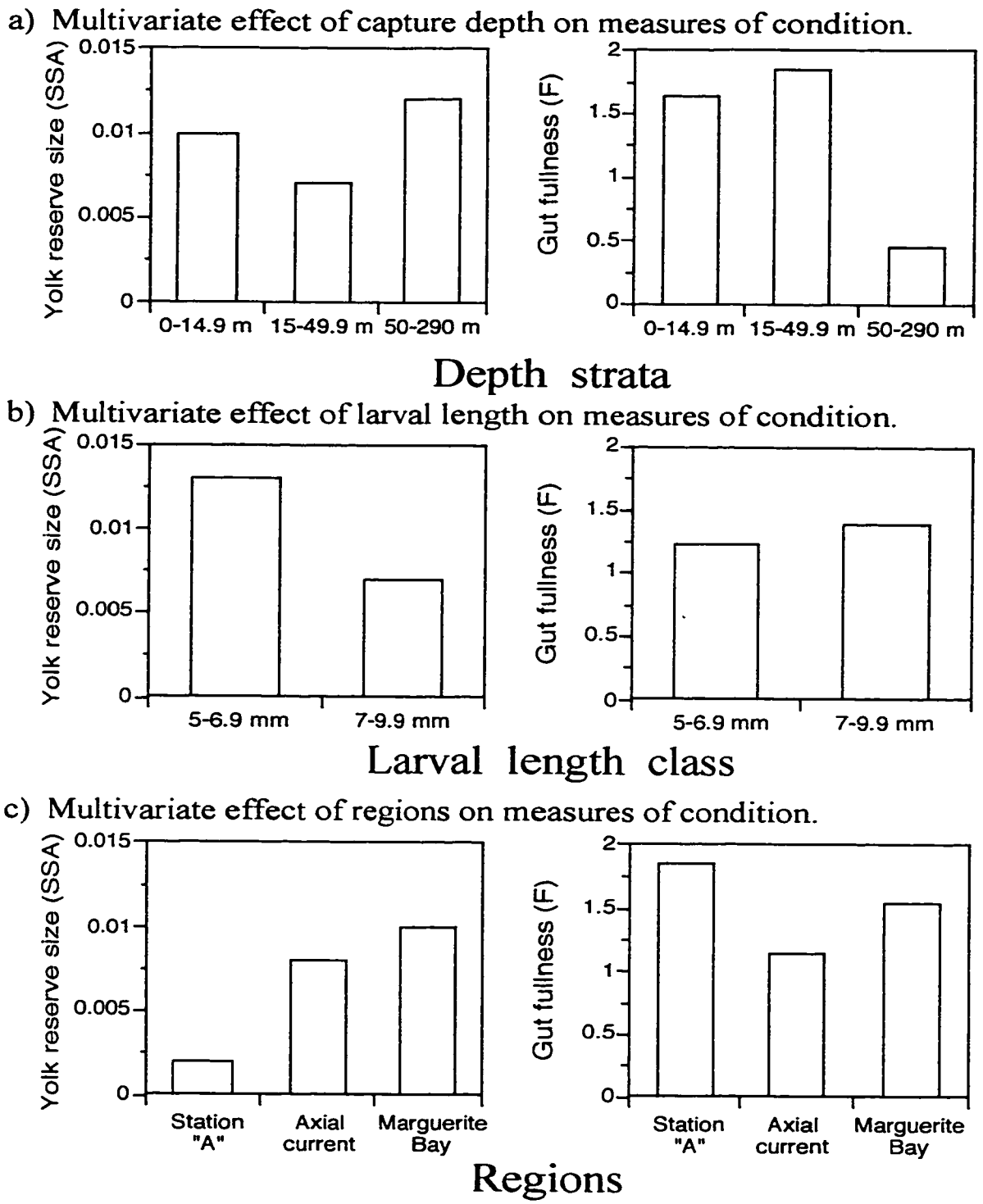


Figure 22. Significant multivariate effects of a) capture depth, b) larval length, and c) regions on condition (*SSA* and *F*) of larval *Trematomus lepidorhinus* collected in late spring.

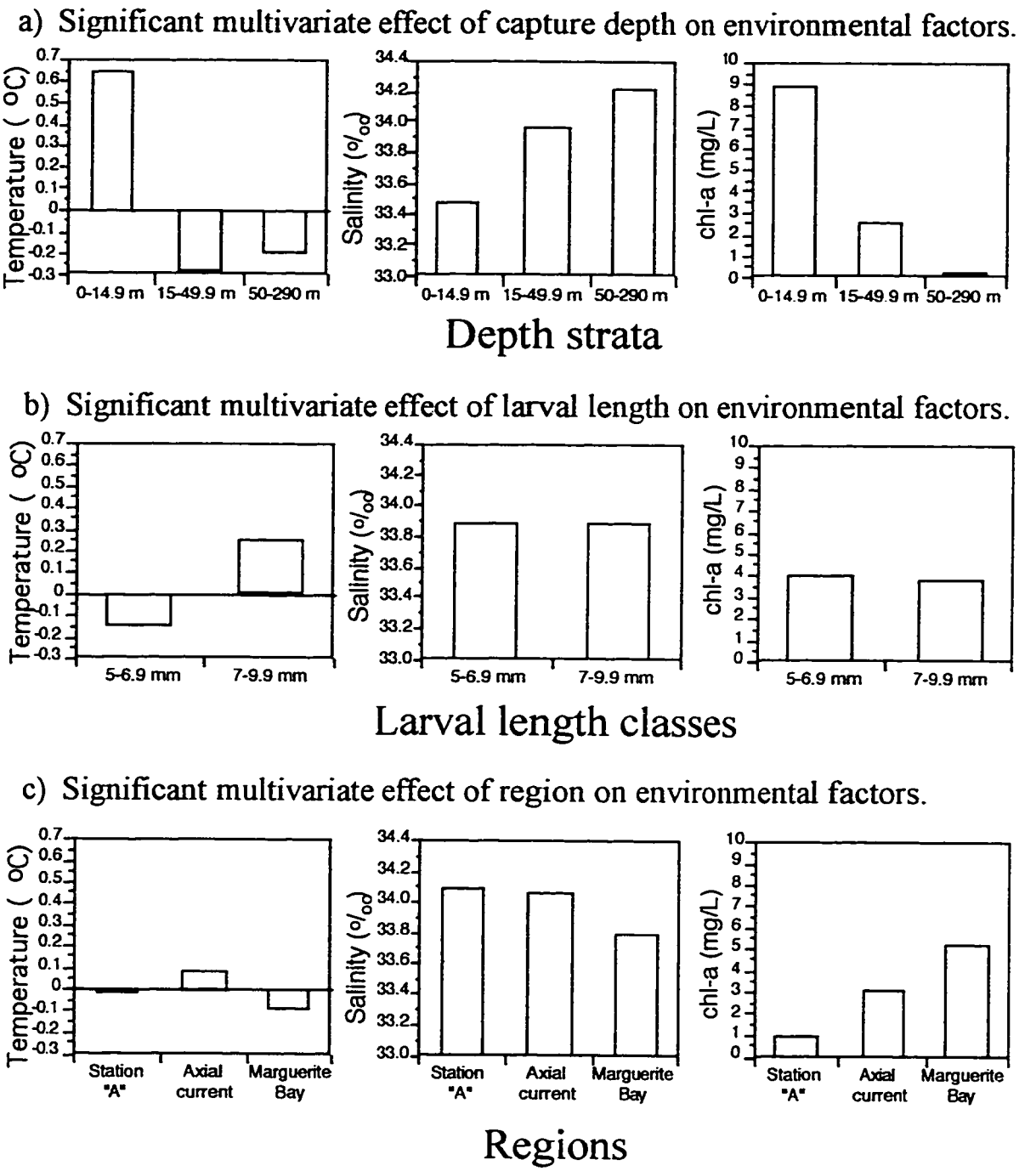


Figure 23. Significant multivariate effects of a) capture depth, b) larval lengths, and c) regions on environmental factors (Celsius temperature, parts per thousand salinity, and milligrams per liter chlorophyll-*a* concentration) for *Trematonus lepidorhinus* larvae collected during late spring.

APPENDIX I

A. Results of backward-stepwise multiple regression analyses.

Lepidonotothen larseni

Dependent variable = Dry Weight
Minimum tolerance for entry into model =0.01

Initial model includes the following independent variables:			
Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	1.99	0.16
3 ED	0.001	0.926	0.337
4 HL	0	0.799	0.372
5 BP	0.001	0.191	0.663
6 BA	0.001	18.205	0
7 IO	0.001	0.236	0.627
8 EDNL	13.232	0.661	0.417
9 HLNL	1.977	0.003	0.959
10 BPNL	6.269	0.089	0.766
11 BANL	6.149	15.788	0
12 IONL	13.688	0.215	0.643

Step #1 R-squared=0.351 Term removed: HLNL			
Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	2.245	0.135
3 ED	0.001	0.931	0.336
4 HL	0	5.723	0.017
5 BP	0.001	0.189	0.664
6 BA	0.001	18.756	0
7 IO	0.001	0.237	0.627
8 EDNL	13.206	0.663	0.416
10 BPNL	6.236	0.087	0.768
11 BANL	6.073	16.123	0

12 IONL	13.661	0.216	0.642
OUT	PART. CORR		
---			
9 HLNL	-0.003	0.003	0.959

Step #2 R-squared=0.351 Term removed: BPNL Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	2.726	0.1
3 ED	0.001	1.277	0.26
4 HL	0	5.719	0.018
5 BP	0	1.401	0.238
6 BA	0.001	18.736	0
7 IO	0.001	0.181	0.671
8 EDNL	12.371	0.957	0.329
11 BANL	6.052	16.098	0
12 IONL	13.156	0.162	0.688
OUT	PART. CORR		
---			
9 HLNL	-0.002	0.001	0.978
10 BPNL	0.019	0.087	0.768

Step #3 R-squared=0.351 Term removed: IONL Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	2.603	0.108
3 ED	0.001	1.119	0.291
4 HL	0	6.022	0.015
5 BP	0	1.381	0.241
6 BA	0.001	22.225	0
7 IO	0	0.044	0.834
8 EDNL	11.459	0.8	0.372
11 BANL	5.757	18.888	0

OUT	PART. CORR		
---			
9 HLNL	-0.002	0.001	0.971
10 BPNL	0.011	0.032	0.858
12 IONL	-0.025	0.162	0.688

Step #4 R-squared=0.35
Term removed: IO

Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	2.76	0.098
3 ED	0.001	1.1	0.295
4 HL	0	6.108	0.014
5 BP	0	1.361	0.244
6 BA	0.001	23.443	0
8 EDNL	11.417	0.783	0.377
11 BANL	5.683	19.665	0
OUT	PART. CORR		
---			
7 IO	0.013	0.044	0.834
9 HLNL	-0.002	0.001	0.976
10 BPNL	0.012	0.034	0.854
12 IONL	0.01	0.024	0.876

Step #5 R-squared=0.348
Term removed: EDNL

Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	13.098	0
3 ED	0	1.331	0.25
4 HL	0	6.282	0.013
5 BP	0	1.216	0.271
6 BA	0	22.705	0
11 BANL	5.572	18.898	0
OUT	PART. CORR		
---			

7 IO	0.01	0.025	0.875
8 EDNL	0.055	0.783	0.377
9 HLNL	0.001	0	0.991
10 BPNL	0.035	0.306	0.58
12 IONL	0.009	0.023	0.881

Step #6 R-squared=0.345 Term removed: EDNL Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	13.083	0
3 ED	0	1.882	0.171
4 HL	0	8.284	0.004
6 BA	0	21.961	0
11 BANL	5.572	18.585	0
OUT	PART. CORR		
---			
5 BP	-0.068	1.216	0.271
7 IO	0.006	0.009	0.925
8 EDNL	0.05	0.636	0.426
9 HLNL	0.009	0.023	0.879
10 BPNL	-0.063	1.033	0.31
12 IONL	0.005	0.008	0.931

Step #7 R-squared=0.341 Term removed: EDNL Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	13.645	0
4 HL	0	7.384	0.007
6 BA	0	20.965	0
11 BANL	5.571	17.89	0
OUT	PART. CORR		
---			
3 ED	-0.085	1.882	0.171
5 BP	-0.082	1.766	0.185

7 IO	0.003	0.003	0.957
8 EDNL	-0.077	1.531	0.217
9 HLNL	0.001	0	0.988
10 BPNL	-0.078	1.572	0.211
12 IONL	0.002	0.002	0.968

The subset model includes the following predictors:
CONSTANT
NL
HL
BA
BANL

Analysis of Variance

Source	DF	F	P
Regression	4	46.662	<0.001*
Residual	408		

Trematomus newnesi

Dependent variable = Dry Weight
Minimum tolerance for entry into model =0.01

Initial model includes the following independent variables.

Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	5.874	0.016
3 ED	0.002	0.274	0.601
4 HL	0.001	1.333	0.249
5 BP	0.001	1.273	0.26
6 BA	0.001	0.417	0.519
7 IO	0.002	3.588	0.059
8 EDNL	26.396	0.165	0.685
9 HLNL	9.623	1.866	0.173
10 BPNL	14.298	1.395	0.238
11 BANL	12.866	0.362	0.548
12 IONL	21.061	3.912	0.049

Step #1 R-squared=0.605 Term removed: EDNL Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	9.318	0.002
3 ED	0	1.767	0.185
4 HL	0.001	1.243	0.266
5 BP	0.001	1.17	0.28
6 BA	0.001	0.379	0.539
7 IO	0.002	3.515	0.062
9 HLNL	9.541	1.762	0.185
10 BPNL	14.131	1.288	0.257
11 BANL	12.808	0.326	0.568
12 IONL	20.991	3.83	0.051
OUT	PART. CORR		
---			
8 EDNL	-0.02	0.165	0.685

Step #2 R-squared=0.605 Term removed: BANL Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	11.332	0.001
3 ED	0.001	1.833	0.176
4 HL	0.001	1.101	0.295
5 BP	0	0.951	0.33
6 BA	0.002	0.383	0.537
7 IO	9.452	3.45	0.064
9 HLNL	13.742	1.6	0.207
10 BPNL	20.964	1.066	0.302
12 IONL		3.774	0.053
OUT	PART. CORR		
---			
8 EDNL	-0.018	0.128	0.721
11 BANL	-0.029	0.326	0.568

Step #3 R-squared=0.605 Term removed: BA Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	11.453	0.001
3 ED	0.001	1.881	0.171
4 HL	0.001	1.105	0.294
5 BP	0.002	0.903	0.342
7 IO	9.443	3.425	0.065
9 HLNL	13.73	1.632	0.202
10 BPNL	20.947	1.05	0.306
12 IONL		3.76	0.053
OUT	PART. CORR		
---			
6 BA	0.031	0.383	0.537
8 EDNL	-0.018	0.133	0.716
11 BANL	0.029	0.33	0.566

Step #4 R-squared=0.604 Term removed: BP Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	12.438	0
3 ED	0.001	1.727	0.19
4 HL	0.002	1.275	0.259
7 IO	9.416	3.836	0.051
9 HLNL	0.938	1.829	0.177
10 BPNL	20.823	1.255	0.263
12 IONL		4.217	0.041
OUT	PART. CORR		
---			
5 BP	-0.047	0.903	0.342
6 BA	0.029	0.333	0.564
8 EDNL	-0.012	0.057	0.812
11 BANL	0.027	0.303	0.582

Step #5 R-squared=0.603 Term removed: BPNL Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	12.254	0.001
3 ED	0.001	1.953	0.163
4 HL	0.001	1.145	0.285
7 IO	9.403	4.378	0.037
9 HLNL	20.692	1.66	0.198
12 IONL		4.82	0.029
OUT	PART. CORR		
---			
5 BP	0.052	1.108	0.293
6 BA	0.048	0.931	0.335
8 EDNL	-0.011	0.05	0.823
10 BPNL	0.056	1.255	0.263
11 BANL	0.046	0.873	0.351

Step #6 R-squared=0.601 Term removed: HL Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	32.374	0
3 ED	0.001	2.018	0.156
7 IO	0.801	4.836	0.028
9 HLNL	20.599	6.813	0.009
12 IONL		5.334	0.021
OUT	PART. CORR		
---			
4 HL	-0.053	1.145	0.285
5 BP	0.049	0.974	0.324
6 BA	0.047	0.884	0.348
8 EDNL	-0.005	0.009	0.924
10 BPNL	0.053	1.125	0.29
11 BANL	0.046	0.849	0.357

Step #7 R-squared=0.599 Term removed: ED Variable	Standard Error	F	P
IN			
---			
1 CONSTANT			
2 NL	0	37.352	0
7 IO	0.001	5.207	0.023
9 HLNL	0.792	8.232	0.004
12 IONL	20.593	5.705	0.017
OUT	PART. CORR		
---			
3 ED	0.07	2.018	0.156
4 HL	-0.055	1.208	0.272
5 BP	0.054	1.186	0.277
6 BA	0.05	1.028	0.311
8 EDNL	0.07	1.977	0.16
10 BPNL	0.057	1.339	0.248
11 BANL	0.049	0.979	0.323

The subset model includes the following predictors:
CONSTANT
NL
IO
HLNL
IONL

Analysis of Variance			
Source	DF	F	P
Regression	1	686.844	<0.001*
Residual	472		

B. Results from iterative non-linear regression analyses for parameter estimation in Le Cren's condition equation.

Lepidonotothen larseni

Non-linear estimation of parameters of Le Cren's condition equation.
Starting values a=0.001, b=2.

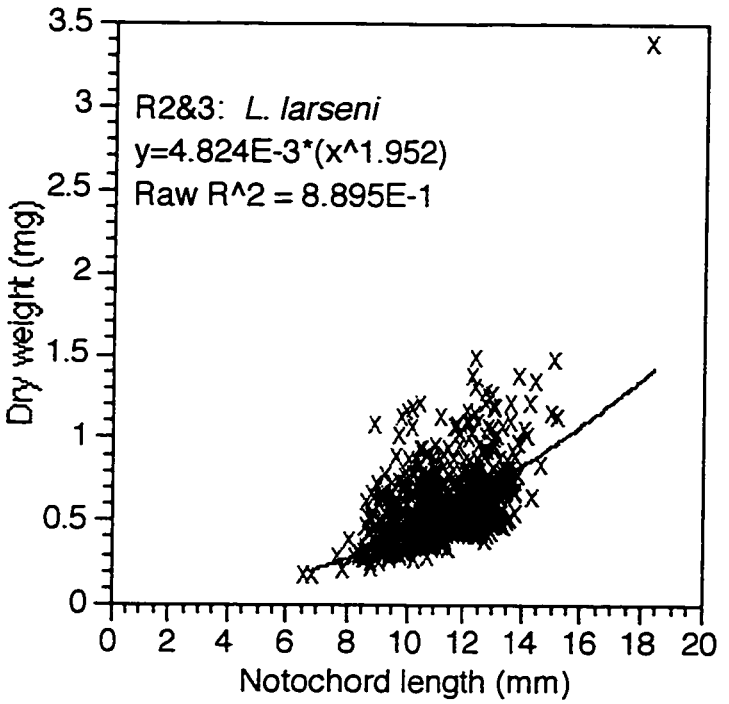
Number of iterations: 26
Dependent variable is Dry Weight

Missing data or estimates reduced degrees of freedom.

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE
REGRESSION	237.4681	2	118.7340
RESIDUAL	27.8950	702	0.0397
TOTAL	265.3635	704	
CORRECTED	39.3606	703	

RAW R-SQUARED (1-RESIDUAL/TOTAL) = 0.8949

PARAMETER	ESTIMATE	LOWER <95%>	UPPER
A	0.0048	0.0020	0.0076
B	1.9524	1.7202	2.1846



Trematomus newnesi

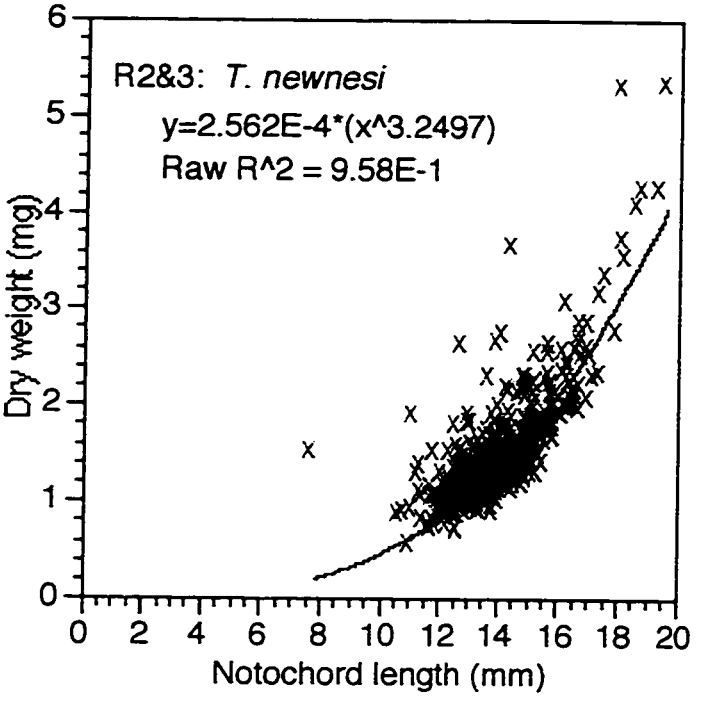
Non-linear estimation of parameters of Le Cren's condition equation.
Starting values a=0.001, b=3.

Number of iterations: 22
Dependent variable is Dry Weight
Missing data or estimates reduced degrees of freedom.

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE
REGRESSION	1225.0384	2	612.5192
RESIDUAL	54.2659	522	0.1040
TOTAL	1279.3050	524	
CORRECTED	168.9099	523	

RAW R-SQUARED (1-RESIDUAL/TOTAL) = 0.9576

PARAMETER	ESTIMATE	LOWER	<95%>	UPPER
A	0.0003	0.0001		0.0004
B	3.2497	3.0735		3.4259



APPENDIX II
RACER II MANOVAs

A) *Lepidonotothen larseni* (RACER II: Early Spring); Bonferroni-corrected α=0.013.

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	1	0.041	0.840
Length class	1	7.685	0.007*
Depth * Length	1	0.048	0.826
Error	108		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	1	2.170	0.144
Length class	1	5.071	0.026
Depth * Length	1	1.545	0.217
Error	108		

Variable (k) Main effects (univariate)	DF	F	P
Depth strata	1	1.027	0.313
Length class	1	0.230	0.632
Depth * Length	1	1.336	0.250
Error	108		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	3, 106	0.038	0.267
Length class	3, 106	0.118	0.008*
Depth * Length	3, 106	0.024	0.462

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	2	3.147	0.046
50-290m vs 0-14.9m and 15-49.9m	1	3.351	0.069
0-14.9m vs 15-49.9m	1	0.139	0.709
Region sampled	1	11.949	0.001*
Depth * Region	2	1.141	0.322
Error	157		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	2	1.867	0.158
50-290m vs 0-14.9m and 15-49.9m	1	3.007	0.085
0-14.9m vs 15-49.9m	1	2.843	0.094
Region sampled	1	0.087	0.769
Depth * Region	2	0.084	0.919
Error	157		

Variable (k) Main effects (univariate)	DF	F	P
Depth strata	2	6.935	0.001*
50-290m vs 0-14.9m and 15-49.9m	1	11.464	0.001*
0-14.9m vs 15-49.9m	1	0.416	0.520
Region sampled	1	7.256	0.008*
Depth * Region	2	0.721	0.488
Error	157		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 308	0.163	0.001*
Region sampled	3, 155	0.143	<0.001*
Depth * Region	6, 308	0.027	0.662

Variable (temperature) Main effects (univariate)	DF	F	P
Depth strata	2	5.252	0.008*
50-290m vs 0-14.9m and 15-49.9m	1	10.242	0.002*
0-14.9m vs 15-49.9m	1	3.874	0.054
Length class	not tested		
Depth * Length	not tested		
Error	62		

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	2	10.758	<0.001*
50-290m vs 0-14.9m and 15-49.9m	1	19.035	<0.001*
0-14.9m vs 15-49.9m	1	11.939	0.001*
Length class	not tested		
Depth * Length	not tested		
Error	62		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	2	31.391	<0.001*
50-290m vs 0-14.9m and 15-49.9m	1	58.541	<0.001*
0-14.9m vs 15-49.9m	1	3.291	0.074
Length class	not tested		
Depth * Length	not tested		
Error	62		

Environmental forcing factors: Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 68	2.293	<0.001*
Length class	not tested		
Depth * Length	not tested		

Variable (temperature) Main effects (univariate)	DF	F	P
Depth strata	2	1.297	0.284
Region sampled	1	0.308	0.582
Depth * Region	2	2.046	0.142
Error	42		

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	2	50.753	<0.001*
50-290m vs 0-14.9m and 15-49.9m	1	85.381	<0.001*
0-14.9m vs 15-49.9m	1	46.499	<0.001*
Region sampled	1	29.240	<0.001*
Depth * Region	2	1.033	0.365
Error	42		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	2	31.226	<0.001*
50-290m vs 0-14.9m and 15-49.9m	1	85.381	0.165
0-14.9m vs 15-49.9m	1	46.499	<0.001*
Region sampled	1	0.002	0.969
Depth * Region	2	4.519	0.017
Error	42		

Environmental forcing factors: Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 78	3.254	<0.001*
Region sampled	3, 40	1.013	<0.001*
Depth * Region	6, 78	0.405	0.022

B) *Trematomus newnesi* (RACER II: Early Spring); Bonferroni-corrected α=0.013.

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	1	4.558	0.035
Length class	not tested		
Depth * Length	not tested		
Error	124		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	1	23.071	<0.001*
Length class	not tested		
Depth * Length	not tested		
Error	124		

Variable (k) Main effects (univariate)	DF	F	P
Depth strata	1	0.578	0.448
Length class	not tested		
Depth * Length	not tested		
Error	124		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	3, 122	0.194	<0.001*
Length class	not tested		
Depth * Length	not tested		

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	2	1.360	0.258
Region sampled	1	4.843	0.029
Depth * Region	2	12.192	<0.001*
Error	306		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	2	5.474	0.005*
15-290m vs 5-14.9m and 0-4.9m	1	1.449	0.230
0-4.9m vs 5-14.9m	1	9.083	0.003*
Region sampled	1	8.462	0.004*
Depth * Region	2	2.933	0.055
Error	306		

Variable (k) Main effects (univariate)	DF	F	P
Depth strata	2	0.829	0.438
Region sampled	1	1.629	0.203
Depth * Region	2	4.377	0.013
Error	306		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 606	0.052	0.017
Region sampled	3, 304	0.050	0.002*
Depth * Region	6, 606	0.134	<0.001*

Variable (temperature) Main effects (univariate)	DF	F	P
Depth strata	2	3.579	0.029
Length class	1	10.643	0.001*
Depth * Length	2	2.459	0.087
Error	267		

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	2	64.645	<0.001*
15-290 m vs 0-4.9 m and 5-14.9 m	1	19.891	<0.001*
0-4.9 m vs 5-14.9 m	1	129.220	<0.001*
Length class	1	1.806	0.180
Depth * Length	2	4.785	0.009*
Error	267		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	2	19.549	<0.001*
15-290 m vs 0-4.9 m and 5-14.9 m	1	10.958	0.001*
0-4.9 m vs 5-14.9 m	1	11.980	0.001*
Length class	1	1.358	0.245
Depth * Length	2	7.244	0.001*
Error	267		

Environmental forcing factors Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 528	0.828	<0.001*
Length class	3, 265	0.040	0.015
Depth *Length	6, 528	0.124	<0.001*

Variable (temperature) Main effects (univariate)	DF	F	P
Depth strata	2	3.257	0.042
Region sampled	2	7.793	0.001*
Gerlache Strait vs station A and Bays	1	13.606	<0.001*
station A vs Bays	1	1.501	0.223
Depth * Region	4	2.273	0.065
Error	118		

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	2	54.91106	<0.001*
Region sampled	2	3.311	0.040
Depth * Region	4	5.062	<0.001*
Error	118		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	2	9.478	<0.001*
50-290m vs 5-49.9m and 0-4.9m	1	1.142	0.288
0-4.9m vs 5-49.9m	1	16.634	<0.001*
Region sampled	2	13.004	<0.001*
Gerlache Strait vs station A and Bays	1	24.558	<0.001*
station A vs Bays	1	12.144	0.001*
Depth * Region	4	3.204	0.015
Error	118		

Environmental forcing factors Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 230	1.091	<0.001*
Region sampled	12, 344	0.323	<0.001*
Depth * Region	6, 230	0.363	<0.001*

C) ***Trematomus lepidorhinus*** **(RACER II: Early Spring); Bonferroni-corrected α=0.013.**

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	1	1.997	0.169
Length class	2	3.008	0.066
Depth * Length	2	1.202	0.316
Error	27		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	1	14.626	0.001*
Length class	2	2.756	0.081
Depth * Length	2	3.063	0.063
Error	27		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	2, 26	0.610	0.002*
Length class	4, 50	0.608	0.041
Depth * Length	4, 50	0.316	0.112

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	1	1.359	0.253
Region sampled	not tested		
Depth * Region	not tested		
Error	31		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	1	8.226	0.007*
Region sampled	not tested		
Depth * Region	not tested		
Error	31		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 606	0.052	0.017
Region sampled	not tested		
Depth * Region	not tested		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	1	0.926	0.419
Length class	not tested		
Depth * Length	not tested		
Error	31		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	1	31.033	<0.001*
Region sampled	not tested		
Depth * Region	not tested		
Error	31		

APPENDIX III
RACER III MANOVAs

A) *Lepidonotothen larseni* (RACER III: Late Spring); Bonferoni-corrected α=0.013.

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	2	0.009	0.991
Length class	1	0.539	0.470
Depth * Length	2	1.126	0.340
Error	26		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	2	1.387	0.268
Length class	1	0.030	0.865
Depth * Length	2	0.137	0.872
Error	26		

Variable (k) Main effects (univariate)	DF	F	P
Depth strata	2	5.664	0.009*
50-290m vs 0-14.9m and 15-49.9m	1	10.710	0.003*
0-14.9m vs 15-49.9m	1	0.127	0.725
Length class	1	0.024	0.878
Depth * Length	2	0.818	0.452
Error	26		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 48	0.650	0.036
Length Class	3, 24	0.023	0.909
Depth * Size	6, 48	0.162	0.713

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	1	1.803	0.192
Region Sampled	2	2.638	0.092
Depth * Region	2	2.562	0.098
Error	24		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	1	2.740	0.111
Region Sampled	2	1.846	0.180
Depth * Region	2	2.047	0.151
Error	24		

Variable (k) Main effects (univariate)	DF	F	P
Depth strata	1	0.080	0.780
Region Sampled	2	0.112	0.895
Depth * Region	2	0.404	0.672
Error	24		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	3, 22	0.196	0.260
Region Sampled	6, 42	0.446	0.182
Depth * Region	6, 42	0.432	0.198

Variable (temperature) Main effects (univariate)	DF	F	P
Depth strata	2	6.487	0.006*
50-290m vs 0-14.9m and 15-49.9m	1	12.965	0.002*
0-14.9m vs 15-49.9m	1	0.759	0.393
Length class	1	1.183	0.289
Depth * Length	2	2.393	0.115
Error	22		

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	2	48.258	<0.001*
50-290m vs 0-14.9m and 15-49.9m	1	96.43	<0.001*
0-14.9m vs 15-49.9m	1	5.509	0.028
Length class	1	0.013	0.910
Depth * Length	2	4.473	0.023
Error	22		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	2	22.968	<0.001*
50-290m vs 0-14.9m and 15-49.9m	1	45.257	<0.001*
0-14.9m vs 15-49.9m	1	1.015	0.325
Length class	1	0.452	0.508
Depth * Length	2	0.440	0.650
Error	22		

Environmental forcing factors Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 38	7.393	<0.001*
Length Class	3, 20	0.113	0.533
Depth * Size	6,38	0.703	0.061

Variable (temperature) Main effects (univariate)	DF	F	P
Depth strata	1	2.921	0.104
Region sampled	2	0.839	0.448
Depth * Region	2	0.953	0.403
Error	19		

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	1	47.705	<0.001*
Region sampled	2	2.373	0.120
Depth * Region	2	0.046	0.956
Error	19		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	1	45.884	<0.001*
Region sampled	2	5.693	0.012*
Rothera vs Gerlache Strait & station A	1	7.010	0.016
Gerlache Strait vs station A	1	2.692	0.117
Depth * Region	2	0.491	0.620
Error	19		

Environmental forcing factors Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 32	5.569	<0.001*
Region sampled	3, 17	2.565	<0.001*
Depth * Region	6, 32	0.167	0.843

B) *Trematomus newnesi* (RACER III: Late Spring); Bonferoni-corrected α=0.013.

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	2	2.375	0.115
Length class	not tested		
Depth * Length	not tested		
Error	28		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	2	1.490	0.243
Length class	not tested		
Depth * Length	not tested		
Error	28		

Variable (k) Main effects (univariate)	DF	F	P
Depth strata	2	0.528	0.596
Length class	not tested		
Depth * Length	not tested		
Error	28		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 50	0.320	0.261
Length Class	not tested		
Depth * Size	not tested		

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	2	0.433	0.652
Region Sampled	2	0.317	0.730
Depth * Region	4	3.373	0.020
Error	34		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	2	1.006	0.377
Region Sampled	2	3.797	0.033
Depth * Region	4	0.827	0.517
Error	34		

Variable (k) Main effects (univariate)	DF	F	P
Depth strata	2	2.934	0.067
Region Sampled	2	0.547	0.584
Depth * Region	4	2.038	0.111
Error	34		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 62	0.345	0.117
Region sampled	6, 62	0.292	0.190
Depth * Region	12, 92	0.799	0.029

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	2	4.334	0.023
Length class	not tested		
Depth * Length	not tested		
Error	27		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	2	4.994	0.014
Length class	not tested		
Depth * Length	not tested		
Error	27		

Environmental forcing factors Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	4, 50	0.621	0.008*
Length class	not tested		
Depth * Length	not tested		

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	2	8.709	0.001*
15-290m vs 0-4.9m and 5-14.9m	1	9.972	0.003*
0-4.9m vs 5-14.9m	1	2.827	0.102
Region sampled	2	26.852	<0.001*
Rothera vs Gerlache Strait & station A	1	53.663	<0.001*
Gerlache Strait vs station A	1	0.332	0.568
Depth * Region	4	3.163	0.026
Error	35		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	2	0.977	0.387
Region sampled	2	9.876	<0.001*
Rothera vs Gerlache Strait & station A	1	19.750	<0.001*
Gerlache Strait vs station A	1	0.266	0.609
Depth * Region	4	0.615	0.655
Error	35		

Environmental forcing factors Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	4, 68	1.034	<0.001*
Region sampled	4, 66	4.549	<0.001*
Depth * Region	8, 66	0.478	0.064

C) *Trematomus lepidorhinus* (RACER III: Late Spring); Bonferoni-corrected $\alpha=0.013$.

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	2	5.479	0.005*
50-290m vs 15-49.9 and 0-14.9m	1	5.751	0.018
0-14.9m vs 15-49.9m	1	3.228	0.075
Length class	1	22.025	<0.001*
Depth * Length	2	1.269	0.285
Error	128		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	2	9.928	<0.001*
50-290m vs 15-49.9 and 0-14.9m	1	17.990	<0.001*
0-14.9m vs 15-49.9m	1	0.307	0.581
Length class	1	0.293	0.589
Depth * Length	2	1.002	0.370
Error	128		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	4, 252	0.191	<0.001*
Length class	2, 127	0.184	<0.001*
Depth * Length	4, 252	0.044	0.239

Variable (SSA) Main effects (univariate)	DF	F	P
Depth strata	2	5.151	0.008*
50-290m vs 15-49.9 and 0-14.9m	1	9.656	0.003*
0-14.9m vs 15-49.9m	1	1.932	0.168
Region sampled	1	11.268	<0.001*
Marguerite Bay vs Coastal Eddy and Axial Current	1	15.365	<0.001*
Coastal Eddy vs Axial Current	1	12.967	0.001*
Depth * Region	4	1.902	0.118
Error	83		

Variable (F) Main effects (univariate)	DF	F	P
Depth strata	2	3.320	0.041
Region sampled	2	1.696	0.190
Depth * Region	4	3.257	0.016
Error	83		

Biological response variables Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	4, 162	0.153	0.017
Region sampled	4, 162	0.316	<0.001*
Depth * Region	8, 162	0.218	0.030

Variable (temperature) Main effects (univariate)	DF	F	P
Depth strata	2	10.689	<0.001*
50-290m vs 15-49.9 and 0-14.9m	1	3.152	0.079
0-14.9m vs 15-49.9m	1	19.193	<0.001*
Length class	1	10.610	0.002*
Depth * Length	2	3.731	0.028
Error	92		

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	2	208.938	<0.001*
50-290m vs 15-49.9 and 0-14.9m	1	351.513	<0.001*
0-14.9m vs 15-49.9m	1	88.615	<0.001*
Length class	1	0.291	0.591
Depth * Length	2	0.841	0.435
Error	92		

Variable ([chl a]) Main effects (univariate)	DF	F	P
Depth strata	2	126.138	<0.001*
50-290m vs 15-49.9 and 0-14.9m	1	210.640	<0.001*
0-14.9m vs 15-49.9m	1	55.251	<0.001*
Length class	1	0.077	0.782
Depth * Length	2	2.836	0.064
Error	92		

Environmental forcing factors Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 178	8.678	<0.001*
Size class	3, 90	0.156	0.004*
Depth * Size	6, 178	0.158	0.034

Variable (temperature) Main effects (univariate)	DF	F	P
Depth strata	2	9.155	<0.001*
50-290m vs 15-49.9 and 0-14.9m	1	7.543	0.008*
0-14.9m vs 15-49.9m	1	13.001	0.001*
Region sampled	2	5.201	0.007*
Rothera vs Gerlache Strait & station A	1	8.713	0.004*
Gerlache Strait vs station A	1	0.549	0.461
Depth * Region	4	0.895	0.472
Error	70		

Variable (salinity) Main effects (univariate)	DF	F	P
Depth strata	2	140.896	<0.001*
Region sampled	2	36.859	<0.001*
Depth * Region	4	4.638	0.002*
Error	70		

Variable (fchl a) Main effects (univariate)	DF	F	P
Depth strata	2	61.265	<0.001*
50-290m vs 15-49.9 and 0-14.9m	1	115.947	<0.001*
0-14.9m vs 15-49.9m	1	15.387	<0.001*
Region sampled	2	12.529	<0.001*
Rothera vs Gerlache Strait & station A	1	16.805	<0.001*
Gerlache Strait vs station A	1	12.750	0.001*
Depth * Region	4	0.619	0.650
Error	70		

Environmental forcing factors Main effects (multivariate)	DF	Hotelling-Lawley Trace Statistic	P
Depth strata	6, 134	6.458	<0.001*
Region sampled	6, 134	1.347	<0.001*
Depth * Region	12, 200	0.320	0.054

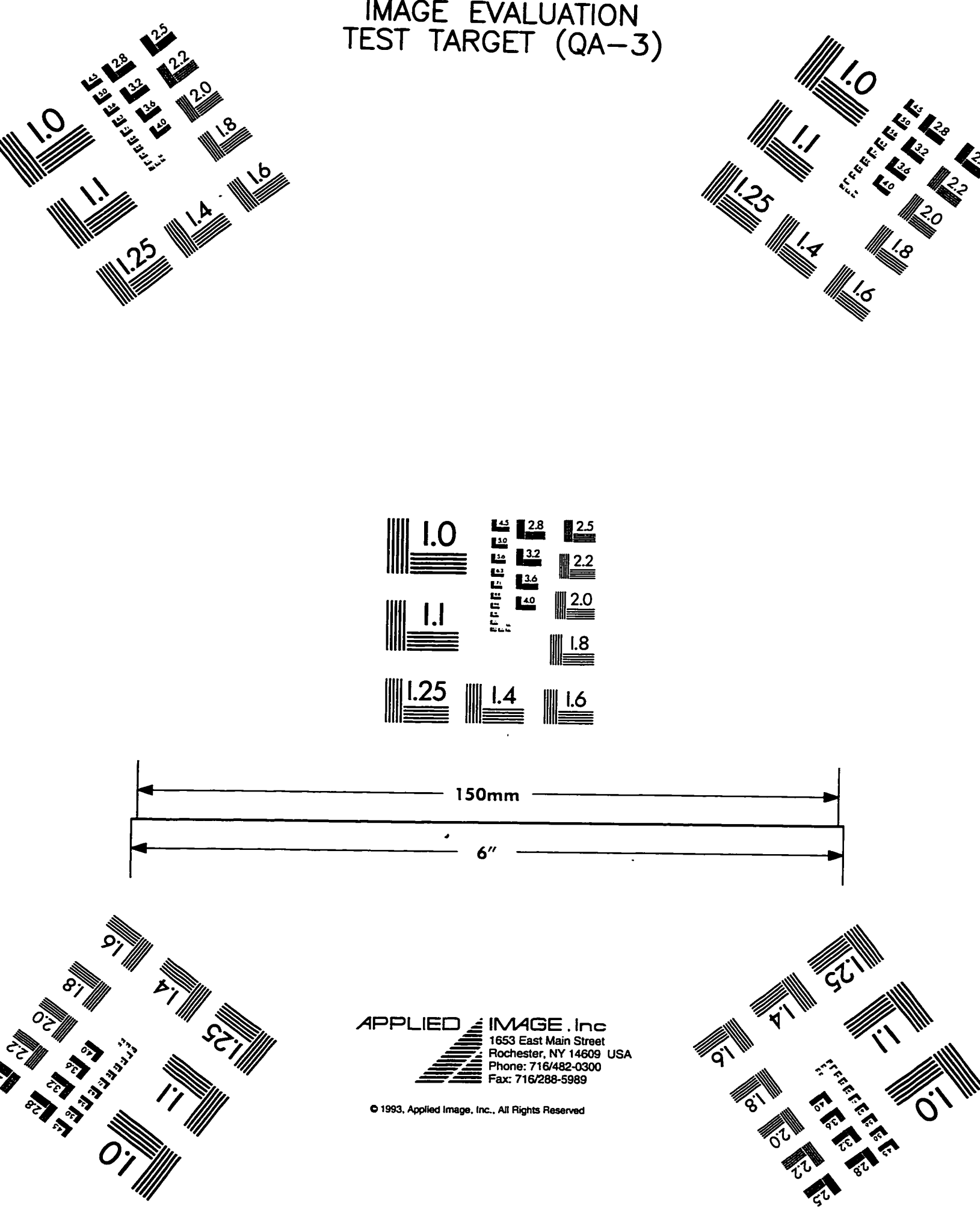


IMAGE EVALUATION
TEST TARGET (QA-3)
1.0
1.1
1.25
1.4
1.6
1.8
2.0
2.2
2.5
2.8
3.2
3.6
4.0
150mm
6"
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